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Synapsids from the Lower Jurassic  
of Western North America

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# THE SKULL AND DENTITION OF TWO TRITYLODONTID SYNAPSIDS FROM THE LOWER JURASSIC OF WESTERN NORTH AMERICA

HANS-DIETER SUES<sup>1</sup>

**ABSTRACT.** Based on an extensive collection of specimens from the Kayenta Formation (Lower Jurassic) of northeastern Arizona, a detailed anatomical account on the skull of two advanced non-mammalian synapsids referable to the family Tritylodontidae is presented. The material is referred to *Kayentatherium wellsi* D. M. Kermack, 1982 and *Dinnebitodon amarali* Sues, 1986, respectively; the skull of the latter form is still poorly known.

The upper postcanine teeth of *Kayentatherium* have two buccal, three median, and three lingual cusps whereas those of *Dinnebitodon* are distinguished by the presence of only two lingual cusps. *Kayentatherium* has but a single pair of upper incisors, which are enlarged and separated by an edentulous gap.

The presence of an internarial bar is demonstrated. The quadrate has a prominent stapedial process and articulates only with the crista parotica (anterior paroccipital process). The quadratojugal is a slender bony rod. The dentary has a very tall coronoid process with a distinctly recurved apex. The postdentary bones form a slender bony rod. The distinct retroarticular process consists of a thin central lamina and a posteriorly thickened rim. The postdentary elements were presumably involved in hearing and are extremely similar to the auditory ossicles in the most primitive mammals.

The skull bears prominent ectocranial crests and has deep zygomatic arches. The lateral wall of the braincase is completely ossified. An extensive secondary palate is formed by the maxillae and palatines in *Kayentatherium* and by the premaxillae and palatines in *Dinnebitodon*. A number of cranial features are consistent with the hypothesis that tritylodontid synapsids were herbivorous. Jaw motion was propalinal and included a significant, posteriorly directed power stroke.

## INTRODUCTION

The question of the origin of mammals has occupied the attention of several generations of anatomists and paleontologists. Extensive collections of advanced "mammal-like reptiles" and early mammals have been brought together from various regions of the world, and, although much detail remains to be clarified, the broader outlines of this important phase in the evolutionary history of the Synapsida are now slowly emerging. There exists a general consensus at present that mammals are derived from the Cynodontia, a paraphyletic assemblage of advanced synapsids of primarily Permian and Triassic age. Kemp (1982) and Jenkins (1984) have reviewed this subject most recently.

Certain Late Triassic and Jurassic representatives of this assemblage already show a host of mammalian characters and indeed have been referred to the Mammalia on occasion. Among these forms, the Tritylodontidae form a well-defined group, which is characterized principally by the possession of multicuspoid molari-form cheek-teeth that meet in precise occlusion. They were classified as primitive mammals with affinities to the Multituberculata by most authors until the 1940s. The discovery of well-preserved and abundant skeletal remains of Tritylodontidae in the Lower Lufeng Series of Yunnan, China (Young, 1940, 1947), now believed to be Early Jurassic in age, and in Liassic fissure-fillings in Somerset, England (Kühne, 1943, 1956) led to a revised assessment of the phylogenetic position of this group. Subsequently tritylodontids were regarded as highly derived descen-

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dants of "gomphodont" cynodonts, combining a number of decidedly mammalian features with obvious specializations for herbivory (Watson, 1942; Crompton and Ellenberger, 1957). Recently, this view has been challenged by Kemp (1982, 1983) who argued for a sister-group relationship between Tritylodontidae and Mammalia (plus possibly Tritheledontidae). Elsewhere, I have reviewed arguments in support of both hypotheses (Sues, 1985a). I prefer the hypothesis that tritylodontids plus gomphodonts form a strictly monophyletic group, Tritylodontoidea (Hopson and Kitching, 1972). The discovery of numerous often admirably preserved and associated skeletal remains referable to three genera of Tritylodontidae from the "Silty Facies" of the Kayenta Formation in northeastern Arizona permits a comprehensive anatomical description of these advanced synapsids. Whatever their phylogenetic relationships may be, tritylodontids display a degree of structural organization comparable to or, in a number of features, even advanced beyond that of forms such as *Probainognathus*, which have commonly been hypothesized as members of the stem-group of the Mammalia. Clearly a detailed anatomical survey of the unusually well-documented Tritylodontidae from the Kayenta Formation is essential to a comprehensive evaluation of the interrelationships of advanced synapsids including mammals.

The present paper describes the skull and dentition in two species of Tritylodontidae from the Kayenta Formation, *Kayentatherium wellsi* D. M. Kermack, 1982 and *Dinnebitodon amarali* Sues, 1986. As anatomical descriptions are most meaningful when they relate skeletal features to soft structures, an attempt has been made to do so where the latter could be restored with a reasonable degree of confidence. Extant primitive mammals provided comparative information concerning neurovascular structures and cranial muscles for this purpose; such compari-

sons are, in my opinion, justified in view of the close relationships, regardless of the preferred hypothesis of tritylodontid affinities.

Most specimens show signs of crushing and other pressure effects, with consequent limitation on the accuracy with which individual illustrations and restorations can be prepared. For the same reasons, exact measurements are not feasible in most instances.

A second paper, in collaboration with F. A. Jenkins, Jr., will deal with the postcranial skeletons of *Kayentatherium* and *Dinnebitodon*. Elsewhere, I have already discussed the phylogenetic status of the Kayenta Tritylodontidae and their possible biostratigraphic significance (Sues, 1986b) and have described cranial remains and teeth referable to a third genus of Kayenta Tritylodontidae, *Oligokyphus* Hennig, 1922 (Sues, 1985b). The latter account includes remarks on jaws and teeth of juveniles presumably referable to *Dinnebitodon* and/or *Kayentatherium*.

The tritylodontid material from the Kayenta Formation collected by the Harvard-MNA field parties since 1977 has been divided between the Museum of Comparative Zoology, Harvard University (MCZ) and the Museum of Northern Arizona (MNA).

## GEOLOGICAL BACKGROUND

Tritylodontid remains were first recovered from the Kayenta Formation in the early 1950s. This material was collected from 8 to 10 feet (2.4 to 3 m) below the top of the formation, just below the presumed contact with the Navajo Sandstone, on Comb Ridge, 6 miles (9.6 km) east of the type locality of the Kayenta Formation near Kayenta, Arizona (G. E. Lewis, 1986). These finds, recently referred to a new genus and species, *Nearctylodon broomi* Lewis, 1986, constituted the first record of this group of non-mammalian synapsids from North America. D. M. Kermack (1982) has described a poorly

preserved skull, the holotype of *Kayentatherium wellsi*, and some other jaw material from a locality near Many Farms, Apache County, Arizona, and a fragment of a very large tritylodontid dentary from Garces Mesa, Coconino County, Arizona. (It should be noted at this point that *Nearctylodon broomi* Lewis, 1986 is a subjective junior synonym of *Kayentatherium wellsi* D. M. Kermack, 1982; this synonymy will be discussed below.) The new specimens described in this paper were obtained from a number of sites in the "Silty Facies" in the middle third of the Kayenta Formation, exposed on Ward Terrace along the Adeii Eechii Cliffs on the land of the Navajo Indian Nation from the region of Dinnebito Wash to Tuba City. Locally these deposits are quite fossiliferous, especially near Gold Spring Wash, and contain a diversified fauna that, in addition to Tritylodontidae, mainly consists of an undescribed new taxon of turtle (Gaffney, Hutchinson and Jenkins, in preparation) and the small armored ornithischian dinosaur *Scutellosaurus lawleri* Colbert, 1981.

The Kayenta Formation is part of the Glen Canyon Group of western North America, a sequence of strata of continental sediments, which are primarily clastic in nature. The depositional basin of the Kayenta sediments, which accumulated on a well-drained lowland floodplain, extends in what are now the areas of northeastern Arizona and central and southern Utah. The source area for the deposits was probably situated in western Colorado, to the east or northeast of the Vermillion Cliffs. The sediments are predominantly red terrestrial and subaqueous claystones, sandstones, and siltstones. Clay pellet conglomerates and limestone form minor strata locally. Tracks of archosaurs, ripple-marked sandstones, and occasional mud-cracked surfaces attest to alternation between shallow water covering and sub-aerial exposure (Callahan, 1951: 54). The "Typical Facies" (Harshbarger *et al.*, 1957:

17) in the eastern part of the area is characterized by irregular ledges of sandstone and grades into the "Silty Facies," a sequence of intercalated claystones, sandstones, and siltstones, in the southwestern part of the Navajo country. The Kayenta Formation varies in thickness from 100 feet (30 m) at Lees Ferry to the east to more than 1,100 feet (330 m) in the Warner Range to the west. Harshbarger *et al.* (1957: 18) report large-scale intertonguing between the Kayenta Formation and the overlying Navajo Sandstone in northern Arizona and southwestern Utah through an interval of up to 700 feet (210 m) and with a lateral extension for at least 100 miles (160 km). This led Lewis *et al.* (1961: 1439) to correlate the lower part of the Navajo Sandstone with the upper portion of the Kayenta Formation, which intertongues with it. Intertonguing has also been observed between the lower part of the Kayenta Formation and the Springdale Sandstone Member of the underlying Moenave Formation (Harshbarger *et al.*, 1957; profile on pl. 2), making them stratigraphical equivalents in several localities in northern Arizona. The two strata are virtually identical in their rock fabric and apparently had the same source and transport direction. Clark and Fastovsky (1986) provide additional geological information concerning the fossiliferous strata and stratigraphic sections at selected localities.

Following Peterson and Pipiringos (1979) and Olsen and Sues (1986), the Kayenta Formation is considered Early Jurassic, rather than Late Triassic, in age. Palynological data from the Whitmore Point Member of the Moenave Formation, which underlies the Kayenta, suggest that the latter is no older than late Sinemurian. The Glen Canyon Group is unconformably overlain by the marine sediments of the San Rafael Group, the oldest beds of which are early Bajocian in age. The biostratigraphical evidence afforded by the tritylodontid synapsids, particularly the presence of *Oligokyphus*, is consis-

tent with this assessment (Sues, 1985b, 1986b).

#### METHODS OF PREPARATION

The majority of specimens were prepared mechanically with the aid of carbide-steel needles and dental burrs of various sizes. Bones with a covering of hematite were partially treated by submersion in a 5 percent solution of  $\text{HSCH}_2\text{COOH}$  (known under the trivial names of mercaptoacetic or thioglycolic acid). Already exposed bone was strengthened with a solution of polystyrene in ethylacetate. The fossils then were submerged in acid for approximately six hours, followed by approximately 18 hours of washing in running water. Softened hematite was removed with the aid of a small brush and fine needles. The procedure was repeated when necessary. Breaks were mended with commercial cyanoacrylate glues.

#### MATERIALS

The principal specimens used in the anatomical descriptions are two skulls referable to *Kayentatherium wellsi* on the basis of their upper dentition (MCZ 8811 and 8812). MCZ 8811 includes an incomplete but excellently preserved skull of a small individual, lacking most of the skull roof, the posterior portion of the right and virtually the entire left zygomatic arch, much of the braincase and the left quadrate and postdentary bones. The tip of the snout is not preserved, and the crowns of the enlarged upper incisors are partially broken off. The specimen has also been subject to some plastic distortion. The conspicuous texture on the bony surfaces of the snout, the presence of replacement incisors, and the rapid increase in buccolingual width of the postcanine teeth posteriorly, along with other features, attest to the immaturity of MCZ 8811. MCZ 8812 includes the virtually complete skull of a very large specimen, with an estimated skull length (measured along the ventral aspect) of *c.* 26 cm (MCZ 8811: *c.*

13.5 cm). Its principal preservational deficiency is considerable lateral crushing of the cranium, particularly affecting the basicranial, occipital, and palatal regions. Aside from its enormous size, maturity of the specimen is indicated by the lack of incisor replacement and a decrease in buccolingual width of the crowns on the posterior upper postcanine teeth.

In addition, other, more fragmentary cranial remains referable to *Kayentatherium* and the still poorly known *Dinnebitodon* were examined. A list of all specimens, including locality coordinates, has been provided by Sues (MS.). Institutional acronyms, preceding specimen numbers, are: MCZ, Museum of Comparative Zoology, Harvard University; MNA, Museum of Northern Arizona, Flagstaff; SAM, South African Museum, Cape Town; UCMP, Museum of Paleontology, University of California, Berkeley; USNM, National Museum of Natural History, Washington, D.C.

#### TERMINOLOGY

The following directional terms are used in the description of teeth: anterior, toward the front of the mouth; buccal, toward the side of the mouth (or cheek); lingual, toward the tongue; posterior, toward the back of the mouth. Otherwise standard anatomical nomenclature has been employed throughout the text.

#### ACKNOWLEDGMENTS

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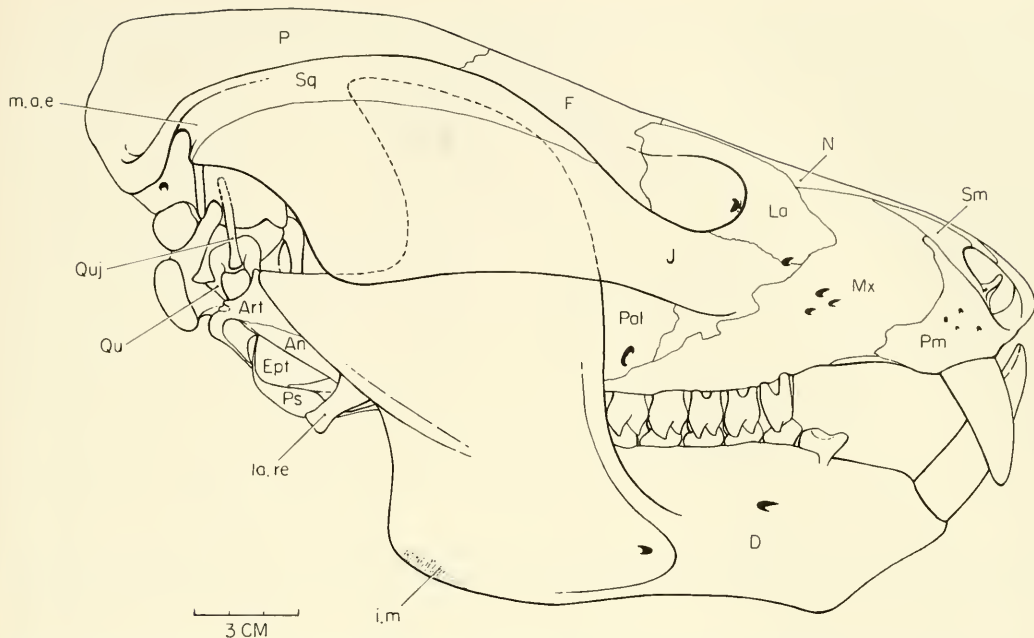


Figure 1. Skull of *Kayentatherium wellesi*, MCZ 8812. Right lateral view. Coronoid process indicated in broken line. Abbreviations for this and the following figures are listed at the end of the text under Appendix.

Lewis and T. M. Bown (Denver), K. A. Joysey (Cambridge), P. Wellnhofer (Munich) and F. Westphal (Tübingen). I owe a special debt of gratitude to A. J. and M. Charig for extending the generous hospitality of their home to me during an extended stay. I am much indebted to W. W. Amaral who has been instrumental during the often extremely difficult preparation of the specimens and who patiently taught me the skills of his craft. I also acknowledge the able assistance by A. H. Coleman (photography) and L. L. Meszoly (labelling).

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ted in partial fulfillment of the requirements for the degree of Doctor of Philosophy to Harvard University in 1983. Since then I have been able to revise and expand parts of this work under tenure of a postdoctoral fellowship in the laboratory of R. L. Carroll at McGill University (Montreal), to whom I am grateful for his continued interest and support.

## SKULL

The skull of *Kayentatherium* (Figs. 1, 2, 4 and 24) has a short and broad snout and a long and narrow postorbital region. The postorbital region of *Dinnebitodon* is apparently relatively shorter (MNA V3223) and its skull proportions are more closely comparable to those of *Bienotherium* as restored by Young (1947). The external nares are separated by an internarial bar. The prominent zygomatic arches enclose long and wide temporal fossae. The temporal fossae are broadly confluent anteriorly with the orbits, which

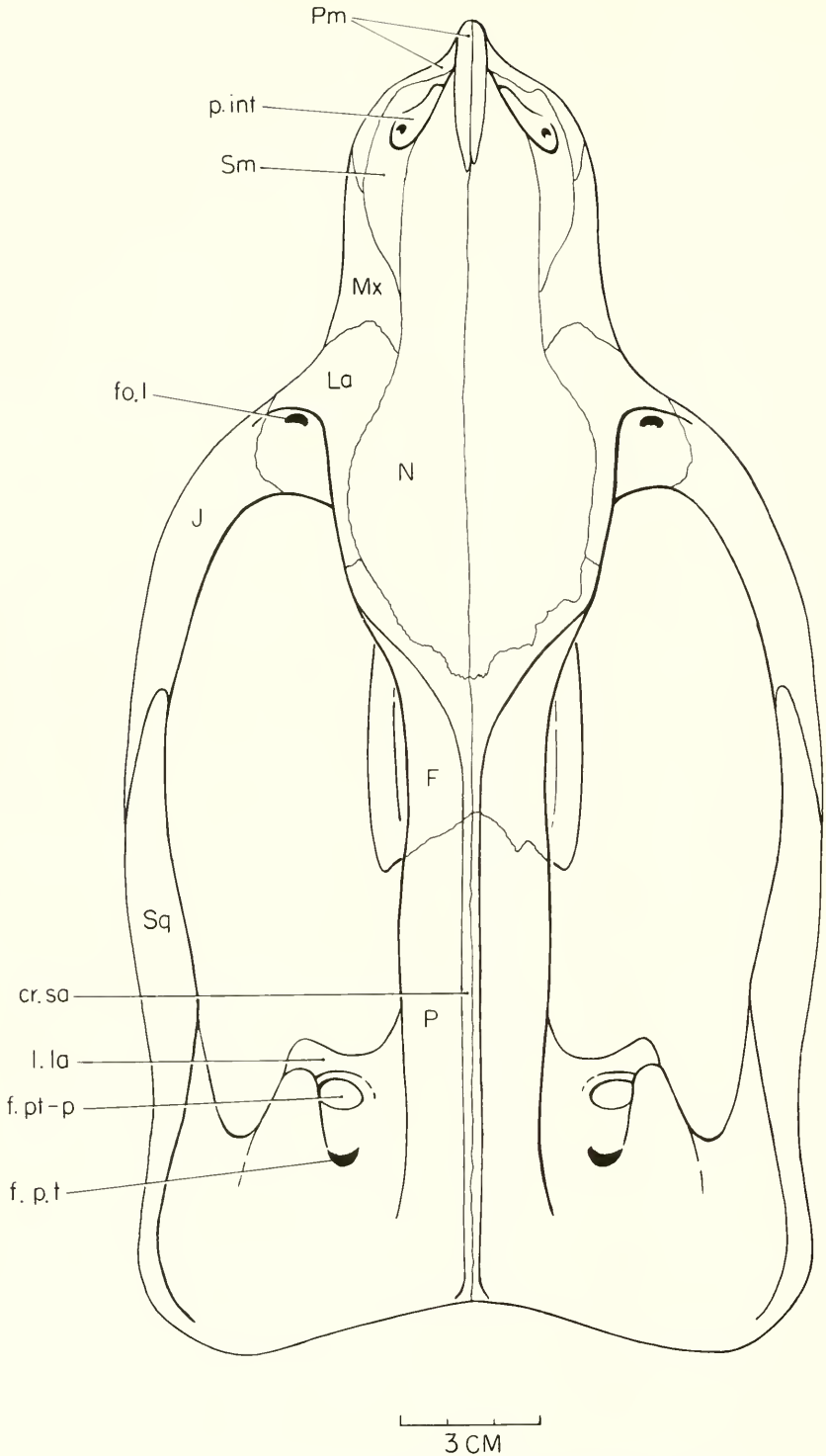


Figure 2. Skull of *Kayentatherium wellsi*, MCZ 8812. Dorsal view, restored.

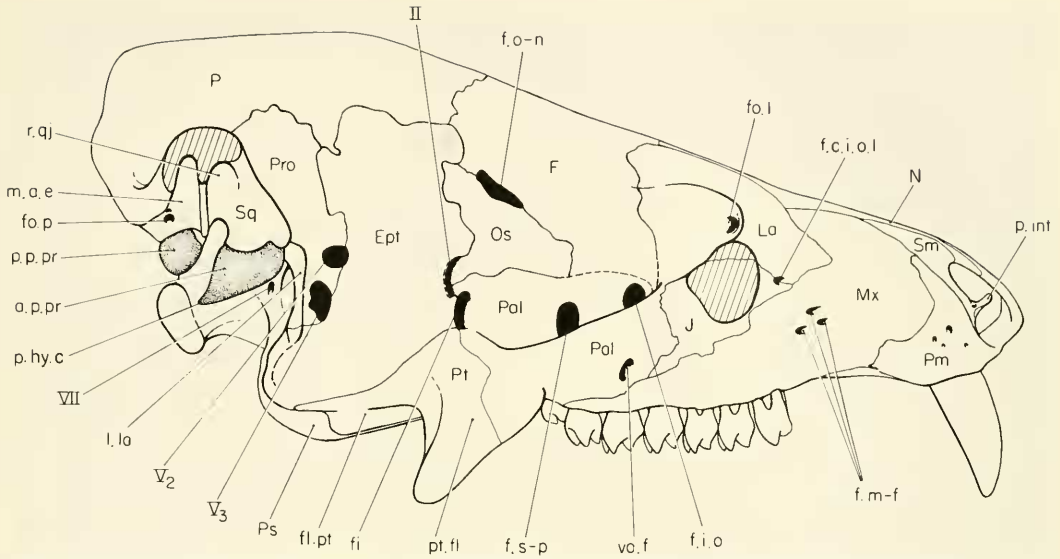


Figure 3. Skull of *Kayentatherium wellesi*, MCZ 8812. Right lateral view, with zygomatic arch and lower jaw removed. Unfinished distal surfaces on paroccipital process indicated by stippling.

are only delimited posterodorsally by bony knobs on the frontals. The posterior portion of the skull bears a distinct sagittal crest and posterolaterally diverging lambdoidal crests. A pineal foramen is absent. The broad and short snout of *Kayentatherium* tapers anteriorly and its sides diverge only little posteriorly. A well-developed secondary bony palate, formed by the maxillae and palatines, extends almost to the posterior end of the upper tooth row in *Kayentatherium* (Fig. 6). The posterior region of the palate shows a rather complex arrangement of longitudinal ridges and channels, reminiscent of that found in many non-therian mammals. The basicranium is broad posteriorly and triangular in ventral view, with the apex of this triangle directed anteriorly. The paroccipital process is robust and divided at its distal (lateral) end. Prominent occipital condyles, formed by the exoccipitals, are situated ventrolateral to the foramen magnum and are separated by a shallow notch for the robust dens. The broadly triangular occipital region is separated from the zygomatic arches laterally by a V-shaped notch on either side.

The lower jaw is characterized by a very

large dentary with a tall and distinctly recurved coronoid process (Fig. 12). The postdentary bones are much reduced and form slender bony rods. They are lodged in a median sulcus on the dentary and articulate with a diminutive quadrate. The reflected lamina on the angular and the retroarticular process are well-developed.

*Kayentatherium* has one greatly enlarged lower incisor in each upper and lower jaw (Figs. 1, 4). In *Dinnebitodon* three (except two in MCZ 8836) upper incisors are developed, the second of which is enlarged (Sues, 1986a: fig. 1). A diastema separates the incisors in both genera from a row of precisely occluding postcanine teeth in both the upper and lower jaws.

*Premaxilla* (Pm). In lateral view, the anteroventral border of the premaxilla rises to form an internarial bridge with its fellow (Figs. 7, 8). The premaxilla is broadly overlapped posterolaterally by a flange from the maxilla as in *Oligokyphus* (Kühne, 1956: fig. 3C), and on the lateral border of the external narial opening it is covered by the large septomaxilla. The dorsolateral exposure of the bone is restricted to a narrow strip that ends in a posteriorly directed point and does not

reach the nasal above (although it extends about 12 mm further back on the left side of the face in MCZ 8812). This condition is comparable to the situation in *Tritylodon* (Simpson, 1928: fig. 1D; Ginsburg, 1962: fig. 4) but unlike *Bienotherium* as illustrated by Young (1947: figs. 1, 2). The palatal portion of the suture between premaxilla and maxilla is distinctly interdigitated. In MCZ 8811 (Fig. 6), the posterior sutural contact with the maxilla extends posteriorly between the first upper post-canine teeth but in the much larger specimen MCZ 8812 the suture extends well anterior to the cheek-teeth as in *Bienotherium* (Young, 1947: fig. 3). The condition in MCZ 8811 foreshadows that in *Dinnebitodon* (MCZ 8830, Fig. 25A) and in *Bienotheroides* (Sun, 1984: fig. 4) where premaxilla and palatine actually exclude the maxilla from participation in the formation of the secondary bony palate. The incisive foramina (f.inc, Fig. 6) are located between the enlarged upper incisors and are completely surrounded by the premaxillae; they were separated by "palatine" processes as in other synapsids. A distinct bony ridge, marking the lateral border of the palatal surface, extends from the enlarged upper incisor to the first post-canine tooth. It coincides with the lateral extent of the palatal portion of the suture between premaxilla and maxilla in *Kayentatherium*.

A slender internarial bar was formed by the long posterodorsal processes of the premaxillae (MCZ 8812; d.p.pm, Fig. 7). Previous authors described the external nares in the Tritylodontidae as confluent but, as is apparent from Young's (1947: 546) account, an internarial bridge was also developed in *Bienotherium*. Much of the posterodorsal processes is missing in the type of *B. yunnanense* but Young's figure 1 shows their posterior ends still wedged between the anterior ends of the nasals.

The sides of the premaxillae just behind the median internarial processes are excavated. The facial portion of the bone is

convex anteroposteriorly as well as dorsoventrally and, in MCZ 8812, shows a number of tiny foramina. The sharp ventral margins of the premaxillae converge anteriorly and enclose between them a transversely concave, triangular area that extends onto the internarial bar anteriorly. The enlarged lower first incisors fit into this gap (Fig. 8).

The first incisor, present only in *Dinnebitodon*, is small and apparently pointed downward and forward. The second incisor is very large and projects more or less vertically downward as in *Bienotherium* (Young, 1947: fig. 2). The third incisor again is only developed in *Dinnebitodon* (with the apparent exception of MCZ 8836). It is much smaller than the preceding one and is situated postero-medial to the latter (Sues, 1986a: fig. 1).

*Septomaxilla* (Sm). The septomaxilla is a large element, overlying the anterior face of the premaxilla on the posterolateral margin of the external naris (Fig. 7). A septomaxillary foramen, commonly developed in more primitive synapsids such as *Procynosuchus* (Kemp, 1979: fig. 3), is absent. The septomaxilla contributes to the floor of the naris ventromedially and extends to the internarial septum as in *Tritylodon* (Simpson, 1928: fig. 1C). The septum nasi in *Tritylodon* (BMNH R8181) is not ossified but is preserved as a gray crystalline substance and was apparently formed in cartilage (Simpson, 1928: 12). This was presumably also the case in MCZ 8812.

A depression (d.p.i) is developed on the anterior surface of the medial portion of the septomaxilla, which forms part of the narial floor and a transverse wall in the posterior part of the naris. It is associated with the prominent shelf-like processus intrafenestralis of that bone (p.int, Fig. 7). Kemp (1979: 96 and fig. 10) has interpreted a similar feature in *Procynosuchus* as the site of Jacobson's organ. Romer and Price (1940: pl. 16, fig. A) place that organ on the posterodorsal aspect of the processus intrafenestralis of the septomaxilla in

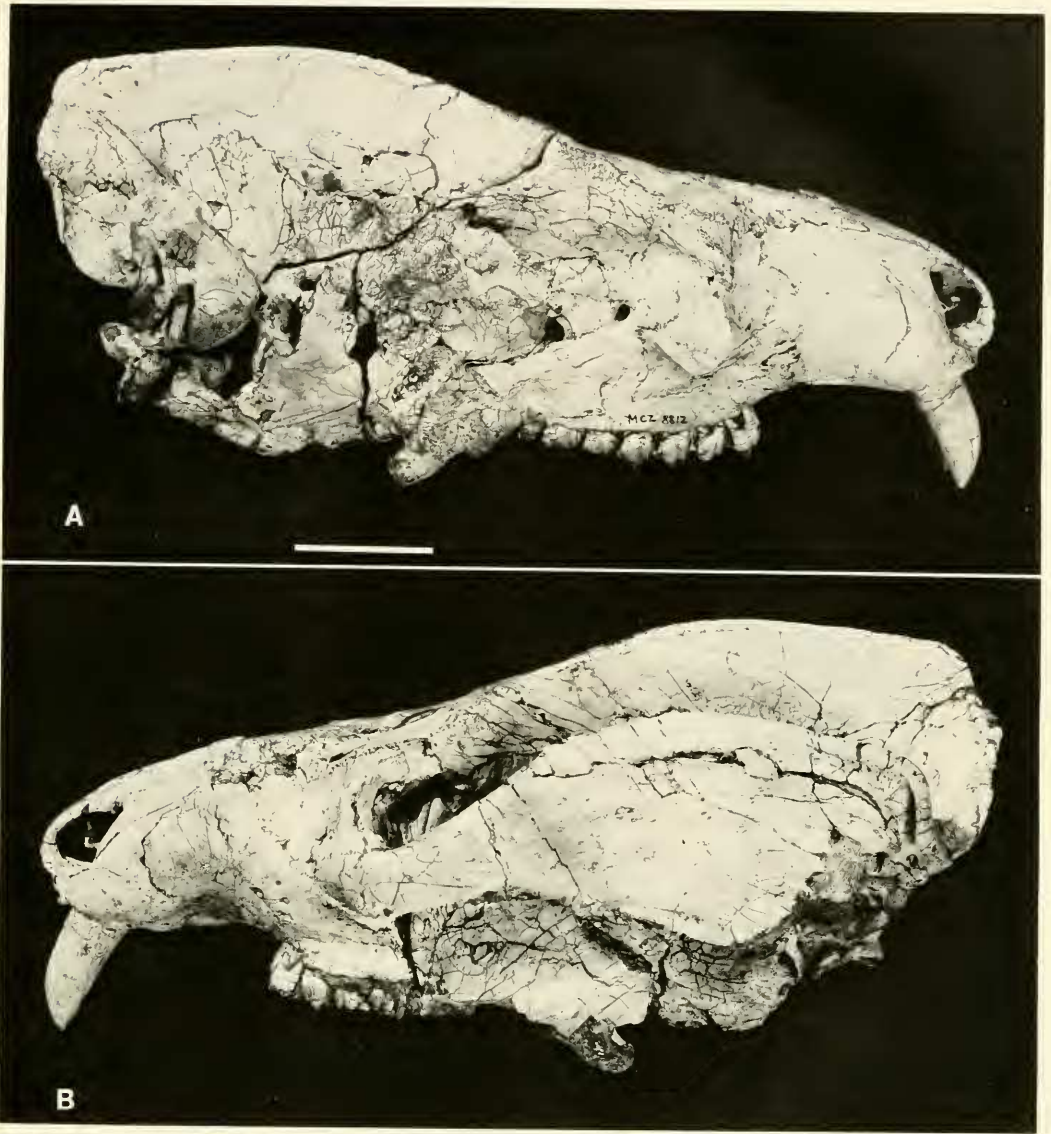


Figure 4. Skull of *Kayentatherium wellsi*, MCZ 8812. A) right lateral view without zygoma. B) left lateral view with zygoma and part of ascending ramus of dentary.

Scale bar. 4 cm.

*Dimetrodon*. This position is also more likely in the Tritylodontidae and, as in many extant mammals, Jacobson's organ may have extended back along the nasal septum (Presley, personal communication). A foramen (c.sm) opening into the

transverse posterior wall of the depression is probably for a nasal branch of N. trigeminus. The processus intrafenestralis turns up as it approaches the mid-line. The elevated median ends of the processes from both sides enclose a space for the

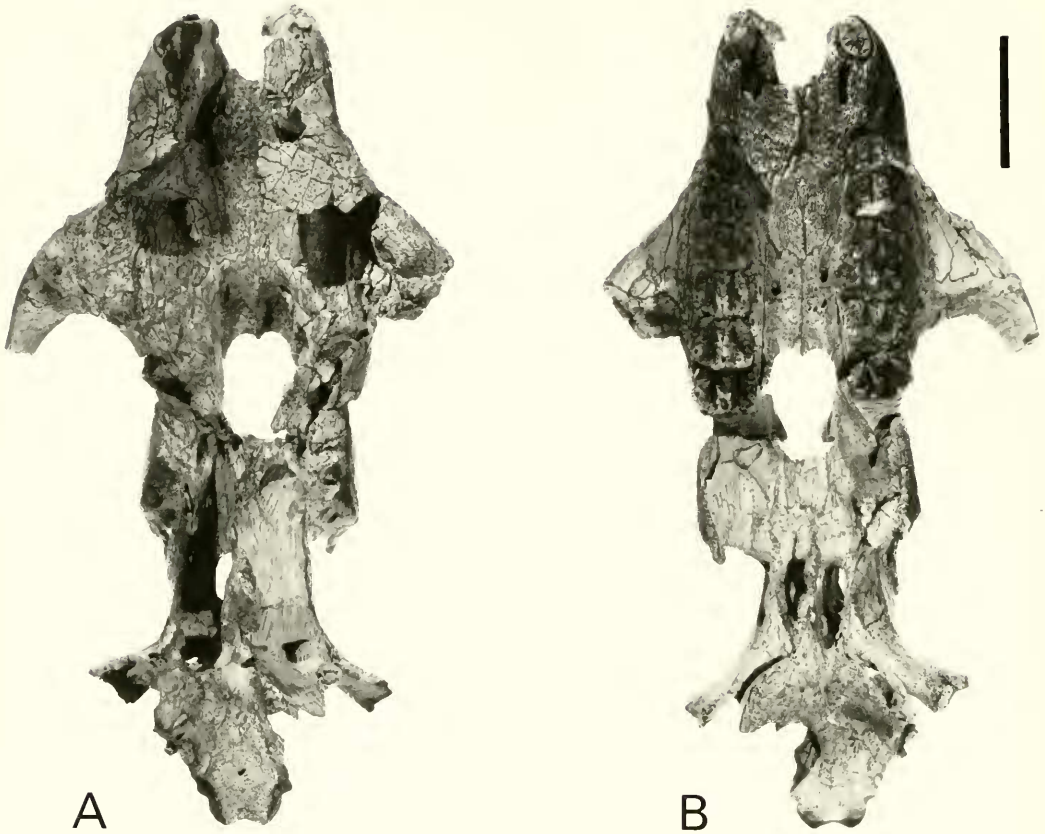


Figure 5. Skull of *Kayentatherium wellesi*, MCZ 8811. A) dorsal view. B) ventral view. Scale bar. 2 cm.

nasal septum (s.s.i). Near its lateral end, the process is obliquely traversed by a short, presumably vascular canal (fo.sm).

**Maxilla (Mx).** The maxilla is the most prominent bone in the facial skull in *Kayentatherium* (Fig. 1) but its lateral and palatal exposure in *Dinnebitodon* is much restricted. It underlies the jugal posterolaterally with a horizontal flange in *Kayentatherium*. The maxilla is overlapped posteromedially by a thin lamina from the palatine and posterodorsally and laterally by the expanded ventral base of the lacrimal. It has a rather short sutural contact with the nasal dorsally (MCZ 8812). The maxilla contacts the dorsal part of the extensive facial portion of the septomaxilla anterodorsally (Fig. 1). In *Dinnebitodon*

(MCZ 8830), the jugal broadly overlaps the maxilla laterally and extends down almost to the level of the upper tooth row (Fig. 25B), much as in *Bienotheroides* (Sun, 1984: fig. 4).

The posterior portion of the maxilla is rather low and is quite thin around the posteriormost cheek-teeth and their roots (Fig. 4). The most conspicuous features of the extensive pars facialis of the maxilla in *Kayentatherium* are the maxillofacial foramina (see below). The bone is recessed anteriorly in front of the first post-canine tooth, probably to provide space for the crown of the forwardly rotated anteriormost tooth before shedding (Fig. 1); this feature is particularly pronounced in MCZ 8811 (mx.r, Fig. 6).

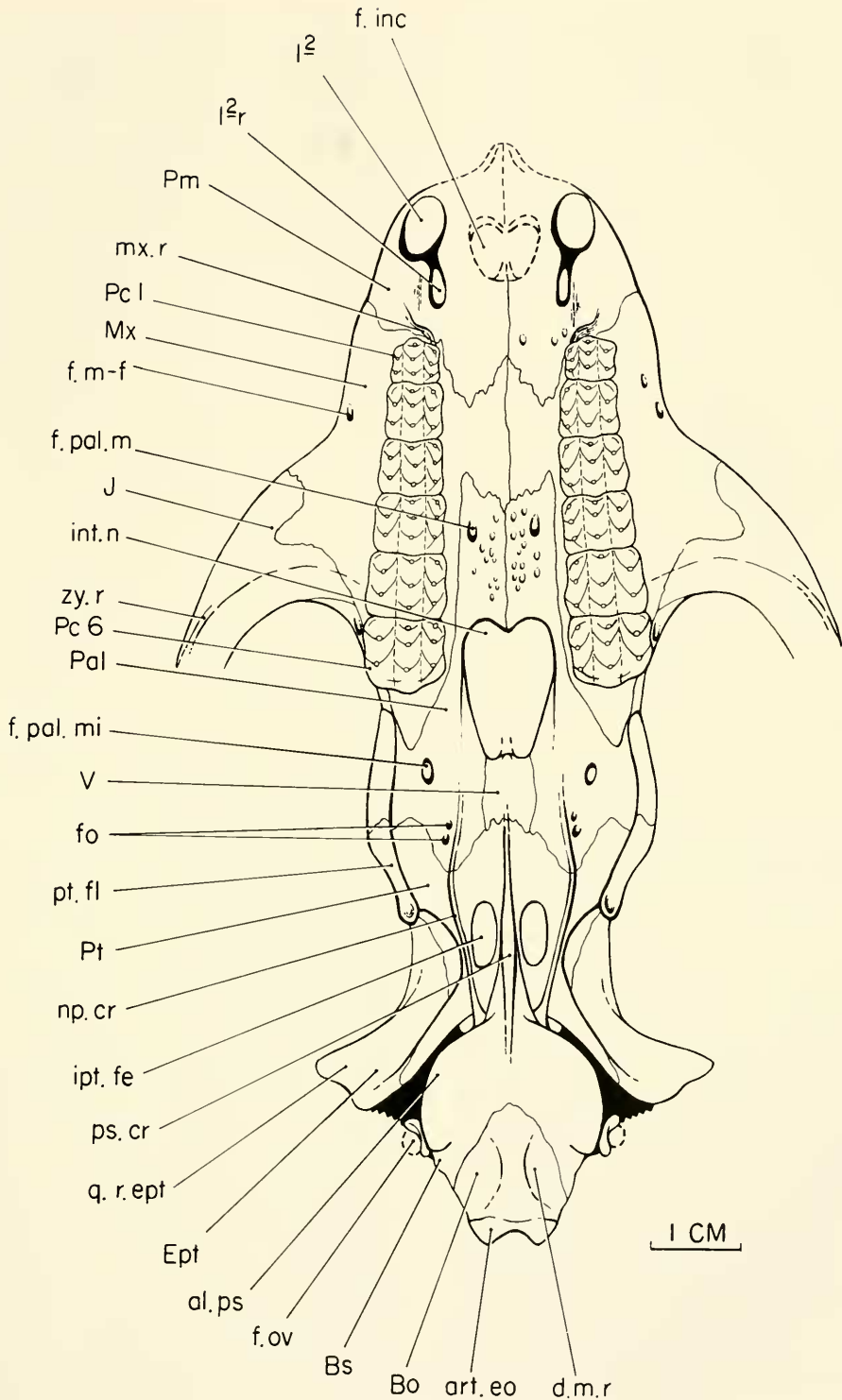


Figure 6. Skull of *Kayentatherium welllesi*, MCZ 8811. Partial reconstruction of skull in ventral view.

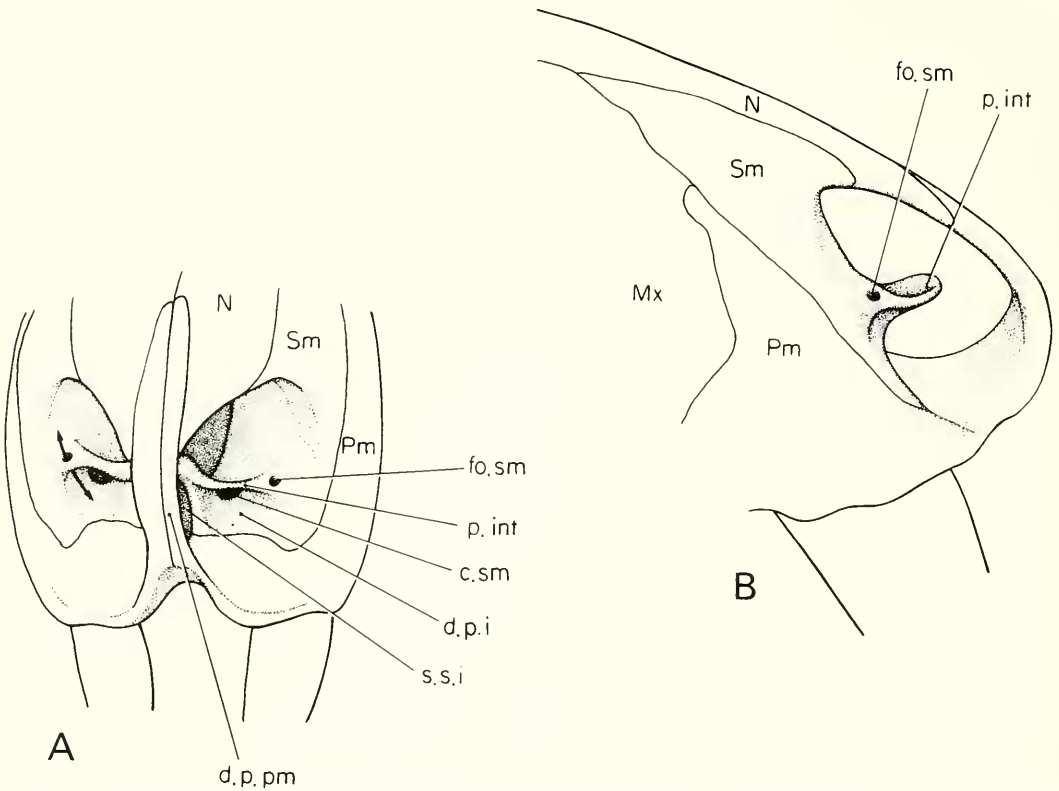


Figure 7. Circumnarial region of the snout in *Kayentatherium wellesi*, MCZ 8812. A) anterolateral view. B) right lateral view.

A large sinus maxillaris (si.mx, Fig. 9) is developed in the medial wall of the maxilla and occupies a position lateral to the entrance of the choana on the dorsal surface of the palate. It forms a deep recess in the inner wall of the maxilla and basal portion of the lacrimal, posterolaterally extending into the root of the zygoma. A partial thin median wall to the sinus is formed by the maxilla anteriorly and by the palatine more posteriorly. Branches of the infraorbital canal system extend on the floor of the sinus (c.i.o., c.i.o.l, Fig. 9). Similar sinuses have been documented in *Thrinaxodon* (Fourie, 1974: 349 and figs. 11A, 12, "MAN") and in *Luangwa* (Kemp, 1980: fig. 7B, "mx. sin.").

The tooth rows of the opposite maxillae are more or less parallel to each other and diverge only little posteriorly (relative to the mid-line; Figs. 5B, 6).

*Infraorbital Canal System and Associated Structures.* This most extensively developed neurovascular canal system to the snout is beautifully displayed in MCZ 8811, an immature specimen of *Kayentatherium*, where much of the skull roof has been eroded away (Figs. 5B, 9).

The canal for ramus maxillaris ( $V_2$ ) of N. trigeminus extends obliquely between the sutural surfaces of the lacrimal and maxilla and continues forward on the floor of the maxillary sinus, much as in *Thrinaxodon* (Fourie, 1974: fig. 13B). At the level of the anterior end of the orbital fossa, it enters the snout (f.i.o, Fig. 3) and divides into an anteriorly extending larger branch and a much smaller lateral branch. The latter terminates in a small foramen (f.c.i.o.l, Fig. 3) above the sixth upper postcanine tooth on the suture between lacrimal and jugal. Kühne (1956: fig. 5A,



“L.V<sup>2</sup>”) and Kermack *et al.* (1981: 17 and fig. 13, “f3”) have observed similar lateral canals terminating on the suture between lacrimal and maxilla in *Oligokyphus* and *Morganucodon*, respectively. *Thrinaxodon* also shows a similar feature (Simpson, 1933: fig. 5). Up to three slit-like maxillofacial foramina (f.m-f, Fig. 3) are developed on the lateral aspect of the maxilla anteroventral to the orbit. They represent exits for branches of the large medial division of V<sub>2</sub> (as in *Oligokyphus*; Kühne, 1956: 27 and fig. 4A, “pEV<sup>2</sup>”) and are homologous to the mammalian infraorbital foramen. Estes (1961: 175–177) has discussed the possible significance of neurovascular foramina on the lateral aspect of the maxilla in forms such as *Thrinaxodon*. He believed that their presence precluded the existence of movable muscular cheeks and lips. *Kayentatherium* shows a concentrated grouping of the maxillofacial foramina well above the alveolar margin, which, according to Estes, may well indicate the presence of a muscular cheek in this genus and other Tritylodontidae.

Posteriorly, N. trigeminus was presumably joined by the ramus palatinus of N. facialis (VII). A deep sulcus (s.v.n, Fig. 9) extends anterolaterally from the region of the vomer to the anterior margin of the orbital fossa. This groove is medially bordered by the orbital flange of the palatine and probably carried N. facialis to the sphenopalatine ganglion, together with various topographically related vessels. A similar groove in the early mammal *Morganucodon* (Kermack *et al.*, 1981: 55 and figs. 46B and D, 50, 100A, “g.Vid.ne”) has been interpreted as carrying the Vidian nerve (i.e., ramus palatinus of VII). A small round pocket (MCZ 8811; d.g.s-p, Fig. 9) near the anterior end of the groove appears to represent the pterygopalatine fossa containing the sphenopalatine ganglion. This identification is supported by the presence of a prominent foramen (f.s-p, Fig. 3) between the orbitosphenoid and the dorsal portion of the palatine, just medial and anterior to the pit, that undoubt-

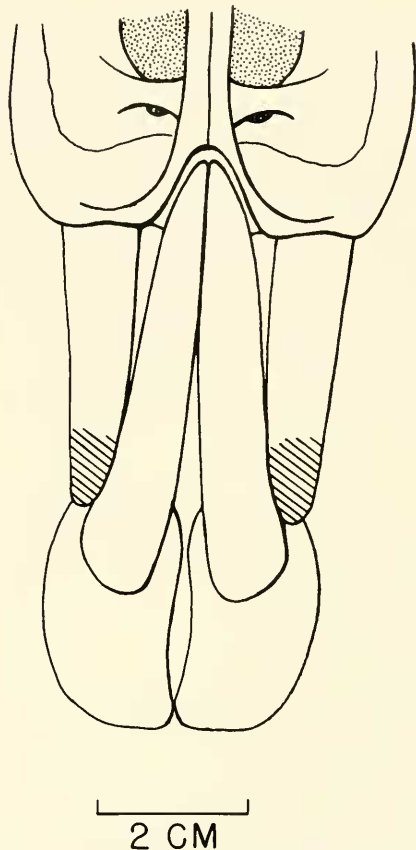


Figure 8. Anterior view of the snout in *Kayentatherium welllesi*, MCZ 8812, to show occlusal relationships of enlarged upper and lower incisors. Hatching denotes wear on upper incisor.

edly represents a foramen sphenopalatinum. Kemp (1980: fig. 7, “sp.pal.f.”) has identified this feature in *Luangwa* and Kermack *et al.* (1981: figs. 46–48, “sph.for.”) in *Morganucodon*. The palatine branch of ramus maxillaris of V, carrying fibers from VII, would have emerged through this foramen, along with A. sphenopalatina. The nerve then probably continued in a shallow groove on the medial aspect of the posterior portion of the palate through the foramen palatinum majus onto the ventral surface of the bony palate (Fig. 6). The greater palatine foramen presumably also served as an exit for A. palatina major as in mammals.

As described by Kühne (1956: 27 and

fig. 5D, "E.L.D.") in *Oligokyphus*, the lacrimal duct ends on the inner side of the lacrimal bone in a funnel. Only a single lacrimal foramen (fo.1, Figs. 3, 9) is present behind the ridge marking the anterior terminus of the orbit. In *Oligokyphus*, as in other cynodont synapsids, the lacrimal duct has two posterior foramina (Kühne, 1956: fig. 5) but only one foramen is present in *Tritylodon* (Simpson, 1928: fig. 1D). The feature called "lachrymal foramen" on the type skull of *Bienotherium yunnanense* (Young, 1947: 547) is obviously misidentified and, if not a mere artifact, probably represents a maxillofacial foramen.

A third canal system is associated with the infraorbital canal but apparently lacks any definite anatomical relation to it. It has also been noted in *Oligokyphus* by Kühne (1956: fig. 5, "Va.") and was interpreted by him as vascular in nature; furthermore, it is present in *Tritylodon* (Broili and Schröder, 1936: 190). A short canal extends posterodorsally from the posteroventral corner of the orbit on the posterolateral aspect of the palatine in both MCZ 8811 and 8812 (va.f, Figs. 3, 9).

*Nasal* (N). The nasal (Fig. 2) is long, flat, and relatively thin. It is narrow anteriorly where it forms the dorsal margin of the external narial opening but becomes much expanded posteriorly between the orbits, comparable to the condition in *Tritylodon* (Simpson, 1928: fig. 1B) and in *Bienotherium* (Young, 1947: fig. 1). Its posterior suture with the frontal is strongly interdigitated.

*Frontal* (F). The most prominent feature of the (in dorsal view) roughly triangular frontal is the median sagittal crest (cr.sa, Fig. 2). It divides anteriorly into two orbital ridges, each of which extends to the anterolateral corner of the frontal to form a rounded postorbital eminence, much as in *Bienotherium* (Young, 1947: fig. 1). The ridges enclose a smooth, flat to gently concave trigon between them. The frontal forms the dorsal rim to and part of the bony wall of the orbit. Both

frontals form a median crest along the ventral surface near their anterior termini, which presumably supported the internasal septum (Tatarinov, 1963: 84). A distinct parasagittal crest, probably for the nasoturbinal (Tatarinov, 1963: 83), is developed on either side of the median ridge.

*Parietal* (P). The sagittal crest reaches its greatest depth on the parietal (Figs. 1, 4). The lambdoidal crests extend posterolaterally and ventrally. The slope of the lateral flange of the parietal is steeply vertical. The parietal is quite long anteroposteriorly and is overlapped ventrolaterally by thin dorsal lappets of the epipterygoid and prootic (MCZ 8812, Figs. 3, 4).

*Lacrimal* (La). The lacrimal (Fig. 3) has an extensive basal portion, which is suturally firmly attached to the maxilla and jugal below, a more dorsolaterally situated part that forms the anterior rim to and the anterolateral wall of the orbit, and has an extensive facial exposure. The bone is penetrated by the infraorbital canal system (see above) near its base and, more dorsally, by the lacrimal duct. The lacrimal sutures in *Dinnebitodon* (MCZ 8830) are very strongly interdigitated, and the lacrimal may have contacted the premaxilla anteriorly as in *Bienotheroides* (Sun, 1984: fig. 3), to the exclusion of the maxilla from the side of the face.

*Jugal* (J). The jugal (Fig. 1) is long and gently curved outward. It arises anteriorly at about the level of the first or second upper postcanine tooth. Its more posterior portion is formed by a deep, nearly vertical, and thin sheet of bone. It further increases in height toward the posterior end where it meets the squamosal along a long, oblique suture. More anteriorly, the squamosal overlaps the jugal laterally, but further posteriorly along the suture, the jugal fits into a groove on the ventral aspect of the squamosal (MCZ 8812). Toward the anterior end of the zygomatic arch (Fig. 1), the jugal rapidly decreases in height and becomes more robust and very wide transversely. Its lateral surface continues the outward curvature of the

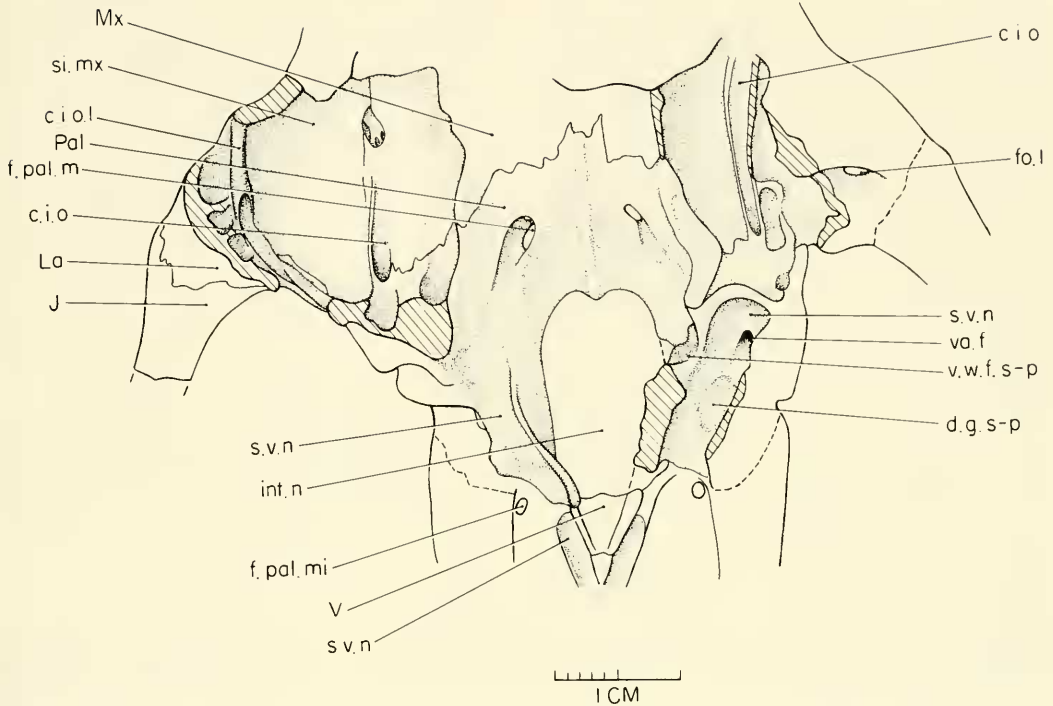


Figure 9. Maxillary sinuses and infraorbital canal system in the snout of *Kayentatherium welllesi*, MCZ 8812, in dorsal view.

bone whereas the dorsal edge turns medially. The anterior root of the zygoma is trihedral in transverse section. Its ventral aspect bears a distinct ridge (zy.r, Fig. 6), probably for the insertion of the pars superficialis of *M. masseter* and homologous to the suborbital process in the tritylodontoids *Exaeretodon* (Bonaparte, 1962: fig. 4) and *Trirachodon* (Crompton, 1963: fig. 10).

**Squamosal (Sq).** The cranial and zygomatic portions of the squamosal (Fig. 2) are separated by a depression that extends from the V-shaped notch in the posterolateral corner of the zygomatic arch to the region above the prominent crista parotica. The dorsal edge of the cranial process, corresponding to the mammalian crista lambdaioidea, extends obliquely posteroventrally to the V-shaped notch and overhangs the occipital plate. The cranial part forms the dorsolateral margin of the post-

temporal fenestra anteriorly. Cranial and zygomatic process join along a broad contact (Fig. 2). The zygomatic portion is quite deep (Fig. 1).

The rounded posterodorsal margin of the zygomatic process overhangs a distinct but rather narrow sulcus that extends along the posterolateral aspect of the squamosal (m.a.e, Figs. 1, 22). This groove expands posteroventrally, resulting in a hollow on the ventral aspect of the posterior zygomatic root. This depression is delimited by the posterolateral portion of the squamosal behind, by the crista parotica (anterior paroccipital process) anteromedially, and a low ridge, which separates it from a large pocket for the proximal end of the quadratojugal, anteriorly. One (MCZ 8842) or two (MCZ 8812, right side) foramina are developed near the posterior margin of the hollow (fo.p, Fig. 3). The squamosal sulcus (m.a.e) probably housed an external

auditory meatus as commonly restored in non-mammalian synapsids (Gregory, 1910: figs. 1, 2; Watson, 1911: figs. 1, 3, "Ex.Au.M."; Kühne, 1956: fig. 10B). Following Presley (1977), I assume that the meatus carried on forward and below from the ventral termination of the bony sulcus (Fig. 22). Just lateral to the crista parotica, a deep pit is developed on the ventral aspect of the squamosal (r.qj); following Kühne (1956: fig. 10B), it is interpreted as a recess for the proximal end of the quadratojugal. An anterior flange of the squamosal overlies the crista parotica (Fig. 3).

*Quadrate* (Qu). The quadrate (Fig. 10) is essentially similar to that of *Oligokyphus* (Kühne, 1956: fig. 9) and *Bienotherium* (Hopson, 1966: fig. 5B). The lateral margin of the quadrate is rounded, not truncated as in *Oligokyphus*, and slightly depressed above the trochlea for contact with the distal end of the rod-like quadratojugal. The trochlea (t.q) is transversely oriented and its articular surface extends onto the anterior aspect of the quadrate. The medial margin of the quadrate is drawn out into a long, tapering, and distinctly posteromedially curved process (m.p.q, Fig. 10), which is deeply excavated anteriorly. This deep anterior recess (st.f) presumably received the distal end of the stapes (Kühne, 1956: 39). Below the groove a distinct facet extends from the medial end of the trochlea to the medial extremity of the stapedial process. The proximal portion of the quadrate is formed by a horizontally expanded, smoothly concave, and upward facing sheet of bone (d.la) that is confluent with the medial surface of the posterodorsal process. The latter process is peg-like and relatively much shorter than that in *Oligokyphus*. A tubercle (a.q.f, Fig. 10A) is formed on the anteromedial margin of the expanded proximal portion immediately above the lateral end of the stapedial groove. It is comparable to the "anterior quadrate buttress" described in *Morganucodon* (Kermack *et al.*, 1981: 105) and may have served as the point of attach-

ment for a ligament. The quadrate only contacted the massive crista parotica (anterior paroccipital process; Crompton, 1964: figs. 6, 8); the same mode of quadrate attachment developed apparently independently in *Morganucodon* and related forms (Crompton and Sun, 1985: 106 and fig. 4C). Comparisons with *Cynognathus* and *Diademodon* suggests that as the squamosal withdrew from the lateral surface of the paroccipital process the bulbous crista parotica extended laterally to form the sole contact with the quadrate (cf. Crompton, 1964: figs. 16, 17).

Kermack *et al.* (1981: 105) emphasize the similarity between the quadrates of *Morganucodon* and *Oligokyphus*. The quadrate of *Kayentatherium* is less similar to that of *Morganucodon*, especially in the prominent development of the stapedial process.

*Quadratojugal* (Quj). The quadratojugal (Fig. 1) is a splint-like bone, which is situated lateral to the quadrate and in close but loose contact with it (MCZ 8812). Its proximal end projects into an anterior pocket on the ventral aspect of the posterior zygomatic root.

*Palatine* (Pal). The extensive horizontal processes of the palatines (Figs. 5, 6) form the posterior portion of the extensively developed secondary palate and the crista choanalis in *Kayentatherium*. The palatine also forms a thin vertical plate of bone, which is closely applied to the medial surface of the maxilla on the sides of the internal nares above the level of the secondary palate. It excludes the maxilla from contact with the pterygoid and ascends to form much of the ventral part of the bony wall to the orbit. Posteriorly, the palatines form a short but distinct spina nasalis posterior (MCZ 8811) for the attachment of the raphe palati (aponeurosis of the palate) as in mammals. The straight lateral sutures anteriorly extend almost parallel to the mid-line suture. The anterior transverse suture between the palatine and maxilla in *Kayentatherium* is strongly serrated and extends posteromedially.

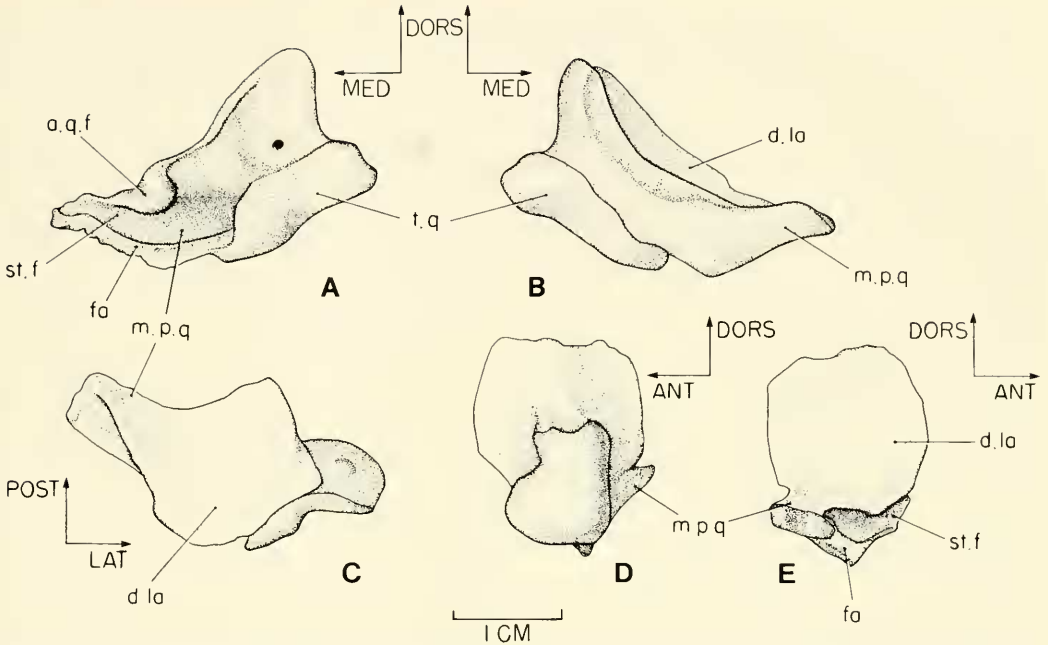


Figure 10. Left quadrate of *Kayentatherium wellsi*, MCZ 8812, oriented in approximate original position. A) anterior view. B) posterior view. C) dorsal view. D) lateral view. E) medial view.

The greater palatine foramen (f.pal.m) lies entirely within the palatine bone on both the dorsal and ventral surfaces of the secondary palate (Figs. 5, 6). It is clearly homologous to the mammalian foramen palatinum majus, which transmits A. palatina major and the palatine branch of  $V_2$ . Numerous minute pits are associated with it in MCZ 8811 but do not penetrate the palatine. A short sulcus extends from the greater palatine foramen anteriorly onto the palatal aspect of the maxilla.

The palate bears a low median ridge or torus (Fig. 5B) that extends forward up to the incisive foramina on the ventral surface. A similar crest, the base of the septum nasi, is developed on the dorsal surface. The horizontal plate of the palatine bone is transversely concave on both its dorsal and ventral faces. Posteriorly, the palatine meets the maxilla laterally, dorsally, and medially, the lacrimal, and the orbitosphenoid. The dorsal portion of the palatine forms a wall to the infraorbital

canal. A small foramen (f.pal.mi) lies posteromedial to the sixth upper postcanine and in front of the suture between the palatine and pterygoid in MCZ 8811 (Fig. 6). It is similar to a foramen in *Morganucodon* that Kermack *et al.* (1981: 56 and fig. 46, "le.pl.for.") interpret as a passage of the lesser palatine nerve. Foramina in this position are also known in *Exaeretodon* (Bonaparte, 1962: fig. 4) and in *Oligokyphus* (Kühne, 1956: fig. 18). Posteromedial to this foramen and just lateral to the pterygo-palatine crest, two additional foramina (fo, Fig. 6) are developed in MCZ 8811. A possibly homologous foramen has been illustrated in *Diademodon* (Watson, 1911: fig. 3). They may have formed exits for pharyngeal branches of the nerves and vessels from the pterygo-palatine fossa supplying the dorsal portion of the nasopharynx. The posterior part of the palatine contacts the unpaired vomer medially. An ectopterygoid is lacking.

*Pterygoid* (Pt). The almost vertical lat-

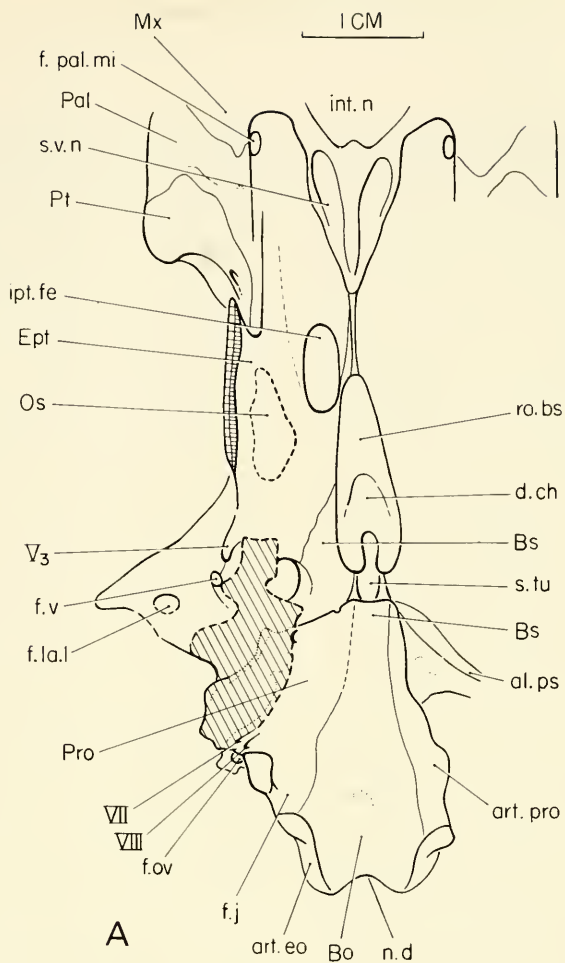
eral flange (pt.fl, Fig. 6) of the pterygoid is distinctly hook-shaped in lateral view and extends well below the level of the upper postcanine dentition. MCZ 8812 has a relatively much smaller flange than MCZ 8811, indicating a pronounced decrease in relative size during ontogeny (compare Figs. 3 and 11B). The convex lateral aspect of the flange is divided by a vertical ridge. Anterior to this ridge, the lateral surface of the pterygoid and of the adjacent region of the palatine shows a distinctive vermiculate texture, which is composed of fine grooves, pits, and ridges, much as on the dorsomedial part of the coronoid (MCZ 8811). A similar sculpturing is also present on the pterygoid of *Oligokyphus* (Kühne, 1956: pl. 10, fig. 2c) and may indicate areas of attachment of specialized connective tissue. A small oval depression of uncertain significance is situated on the lateral aspect of the medially curved distal extremity of the lateral flange in MCZ 8811. The convex external surface of the pterygoid flange lies behind and slightly medial to the buccal row of cusps on the posterior postcanine teeth (Fig. 6). The internal face of the lateral flange is distinctly concave anteroposteriorly and dorsoventrally. A short posterior ramus of the pterygoid extends posterolaterally on the ventral aspect of the posterior extension of the epipterygoid; neither reaches the quadrate.

The medial edge of the pterygoid turns upward to approach the basipterygoid joint. The pterygoids form the anterior portion of a prominent keel along the ventral aspect of the cranium, commencing behind the vomer and continued posteriorly by the parasphenoid (ps.cr, Figs. 6, 11B). On either side of this keel and enclosing a median trough with it, there is a sharp bony crest (np.cr, Fig. 6) formed by the pterygoid posteriorly and extending onto the palatine anteriorly. This nasopharyngeal crest runs more or less parallel to the median keel and probably defined the lateral boundary of the ductus naso-pharyngeus whereas the median keel

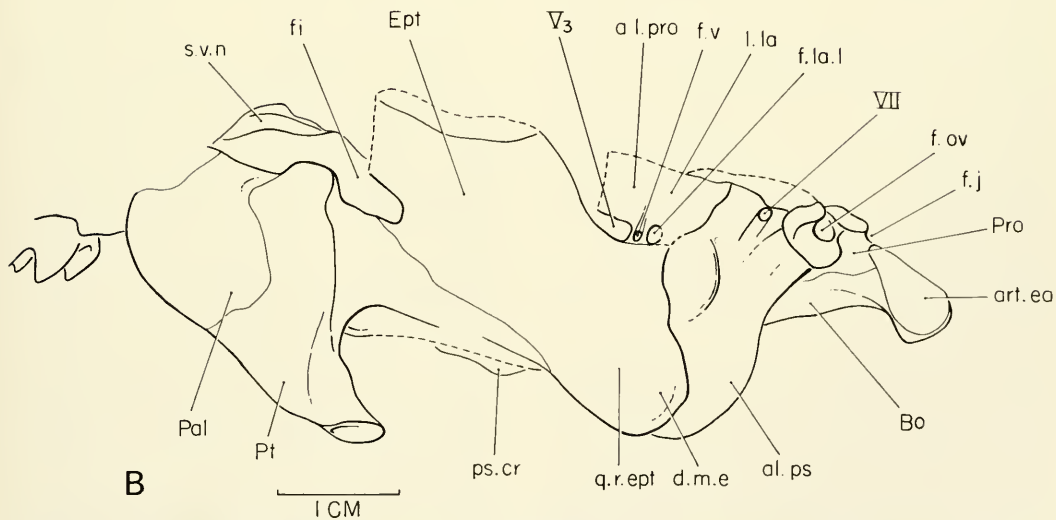
possibly formed the attachment for the median raphe for the pharyngeal constrictors. The pterygo-palatine crest encloses a lateral trough with the lateral flange of the pterygoid. The entire configuration of longitudinal crests very closely resembles the system of ridges and troughs on the posterior portion of the palate in certain non-therian mammals (Multituberculata: Kielan-Jaworowska, 1970: 975; *Morganucodon*: Kermack *et al.*, 1981: figs. 51A, 98). As in *Morganucodon*, the median keel does not extend into the internal nares but a cartilaginous nasal septum surely was developed. The septum is ossified in *Cynognathus* (Broili and Schröder, 1934: fig. 3) and in multituberculates and *Ornithorhynchus* (Kermack *et al.*, 1981: 60). The lateral trough in *Kayentatherium* is wider and more shallow than in *Morganucodon* and the median troughs are confluent at their anterior termini well behind the choana, different from the condition restored in *Morganucodon*. Kielan-Jaworowska (1970: 975) has interpreted the lateral troughs in multituberculates as areas for muscle attachment, specifically for M. tensor veli palatini, and the median troughs as respiratory passages. Barghusen (1986) disagrees with this restoration and regards the lateral troughs as passages for the eustachian tubes. This would be consistent with Presley and Steel's (1978: 106) suggestion that the lateral flange of the pterygoid is homologous to the hamulus pterygoidei of the mammalian ala temporalis. The configuration of this region of the palate might represent an essentially mammalian pattern.

A distinct posterolateral flange is developed along the posterior ramus of the pterygoid (fl.pt, Fig. 3). A comparable feature has not been reported previously in any non-mammalian synapsid. It possibly served as the site of origin for an equivalent of the mammalian medial (internal) pterygoideus and/or tensor tympani muscle.

*Basisphenoid and parasphenoid* (Bs). In absence of clear sutural delineation be-



A



B

Figure 11. Incomplete basicranium of *Kayentatherium welllesi*, MCZ 8811. A) partial dorsal view. B) left lateral view. Hatching denotes broken surfaces; broken lines indicate incomplete edges.

tween the basisphenoid and parasphenoid they are described here as a single element. They, together with a possible presphenoid component, form a large median ossification that floors much of the braincase anterior to the sella turcica. This sheet-like ossification is very deep vertically, especially at the point of convergence of the parasphenoid wings (al.ps, Fig. 6). The sella turcica (s.tu, Fig. 11A) is a distinct oval depression in the dorsal face of the basisphenoid, much as in *Oligokyphus* (Kühne, 1956: pl. 5, fig. 3a), and has sharp dorsal edges except posteriorly where A. carotis interna entered the sella. Above and lateral to the pituitary fossa, a small foramen is developed on either side; it presumably marks the exit for N. abducens (VI) as in *Oligokyphus* (Kühne, 1956: 53). More lateral, a small vascular canal extends vertically down along the median wall of the cavum epiptericum. The basisphenoid forms a low median keel ventral to the sella turcica. Immediately anterior to the sella, however, it forms a very deep but delicate rostrum (ro.bs, Fig. 11A), comparable to spur-like features in this position in cf. *Scalenodon* (Parrington, 1946: fig. 7B, "B PR") and in *Bienotherium* (Hopson, 1964: fig. 3) and to Hahn's "tuberculum sellae" in the paulchoffatiid multituberculate *Pseudobolodon* (Hahn, 1981: 235). The posterodorsal portion of this rostrum forms an expanded, transversely concave surface (d.ch, Fig. 11A), possibly for chiasma n. optici (Stadtmüller, 1936: 912) and comparable to a depression on the tuberculum sellae in *Pseudobolodon* (Hahn, 1981: fig. 4, "foh"). The rostrum is anteriorly continuous with the large orbitosphenoids (MCZ 8812).

In immature specimens of *Kayentatherium* (MCZ 8811 and USNM 317203), a large oval opening (ipt.fe, Figs. 6, 11A) is developed in the floor of the cavum cranii anterior to the basipterygoid process. Its margins are largely defined by the posterior portion of the pterygoid. True interpterygoid vacuities were previously

known in the much more primitive *Procyonosuchus* (Kemp, 1979: fig. 12) and, among advanced synapsids, in the tritheledontid *Chalimia* (Bonaparte, 1980: fig. 4). Small openings in a similar position have been noted in a juvenile of *Thrinaxodon* (Estes, 1961: fig. 2, "iv"), and their presence in MCZ 8811 and USNM 317203 appears to attest further to the immaturity of these specimens. These features may be homologous to the foramina labelled "vid.c." in *Luangwa* by Kemp (1980: fig. 9A) and "FOR" in *Exaeretodon* by Bonaparte (1962: fig. 4) and mark the re-entry into the skull of the ramus palatinus of N. facialis (Parrington, 1946: 184).

The cultriform process of the parasphenoid is very narrow and has a deep ventral keel (Fig. 11B) along its entire length. The keel has an arcuate ventral margin and reaches its greatest depth between the interpterygoid vacuities in MCZ 8811. The parasphenoids form large posterolateral wings or alae, which enclose a broad and transversely concave posteromedian surface between them (al.ps). The considerable development of the alae is presumably related to the substantial hypaxial flexor musculature for the large head. The wings also provide a partial floor to the cavum epiptericum.

*Orbitosphenoid* (Os). The homology of this large bone (MCZ 8812; Fig. 3) with the orbitosphenoid of therian mammals is uncertain. As in monotremes (Kuhn, 1971: 86), the element in question is not suturally separated from the remainder of the sphenethmoid complex but it can be identified on the basis of topographical criteria. It is called orbitosphenoid here, following Bonaparte (1962: 159) and Hopson (1964: 14). In the Anomodontia, a similar extension of the sphenethmoid forms part of the lateral wall of the braincase (e.g., *Lystrosaurus*; Cluver, 1971: fig. 2). In both Tritylodontidae (MCZ 8812) and Tritheledontidae (Crompton, 1958: 195), the orbitosphenoid contacts the prootic posteriorly at the dorsal end of the pila antotica.

The posterior part of the orbitosphenoid



noid lies well medial to the epipterygoid. Anteriorly, its lateral wings contact the orbital portion of the palatine anteroventrally and the frontal anteriorly. Each lateral wing is rather thin. Anterodorsally, it forms the posterior margin of a large foramen orbitonasale (f.o-n, Fig. 3; for the passage of both N. and A. ethmoidalis), similar to that in *Exaeretodon* (Bonaparte, 1962: fig. 5, "FOR.ETH?") and in *Tachyglossus* (Kuhn, 1971: fig. 37). N. opticus (II) emerged through a short canal between the anterior margin of the epipterygoid and the orbitosphenoid above the fissura orbitalis (Fig. 3). The lateral wings of the orbitosphenoid converge on each other posteriorly and become continuous with the sphenethmoid complex. The resulting structure, an extensive ossified septum interorbitale, is thin except dorsally where the wings form a trough. This dorsal trough presumably corresponds to the embryonic planum suprseptale and formed a floor to the anterior portion of the brain, much as in *Bienotherium* (Hopson, 1964: 14) and *Exaeretodon* (Bonaparte, 1962: 159; Bonaparte 1966: fig. 6B).

*Epipterygoid* (Ept). The ascending part of the epipterygoid (Figs. 3, 11B) is a wide and tall sheet of thin bone that forms a substantial portion of the secondary lateral wall of the cavum cranii. The lamina is especially expanded along its dorsal margin where it broadly overlaps the posteroventral part of the frontal and the ventrolateral portion of the parietal (MCZ 8812). The fissura orbitalis (fi) produces a fairly large emargination in the anterior border of the epipterygoid bone. A smaller incisure is made further dorsally by the foramen for N. opticus (II). The posterior edge of the ascending process forms the anteroventral margin of the foramen for  $V_2$  and the anterior margin for the exit of  $V_3$ . The remainder of the margins of these foramina is formed by an anterior extension of the prootic.

Presley and Steel (1976) have challenged the widely accepted homology of

the mammalian ala temporalis with the ascending process of the epipterygoid in advanced non-mammalian synapsids. They noted that the former separates the exits for the mandibular and maxillary branches of N. trigeminus whereas in the latter both rami emerge behind the processus ascendens. Presley and Steel (1976: 453) claimed the presence of a short process from the epipterygoid participating in the formation of a bony partition between the two trigeminal foramina in a specimen of "*Trirachodon*" (=cf. *Scalenodon*), which is housed in the University Museum of Zoology, Cambridge University. They regarded this process as the precursor of the mammalian ala temporalis. I found no indication of such a process in the new material of *Kayentatherium* or in their specimen; in all these examples, the epipterygoid forms the anterior margins of the trigeminal foramina. The mammalian alisphenoid possibly includes the processus ascendens of non-mammalian synapsids and part of the anterior lamina of the periotic. This hypothesis is fully consistent with various embryological demonstrations of more than one center of development in the mammalian alisphenoid (Presley, personal communication).

Below the orbital fissure, a slender process of the epipterygoid extends medially to the lateral flange of the pterygoid. The deep, flange-like posterior process of the epipterygoid (q.r.ept, Fig. 11B), homologous to the quadrate ramus in *Thrinaxodon*, sharply turns posterolaterally behind the sutural contact with the basisphenoid at an angle of about 45° from the sagittal plane (Fig. 6), much as in *Bienotherium* (Hopson, 1964: fig. 2). The rounded posterior margin of each posterior flange is turned outward and forms a somewhat thickened edge. A distinct depression (d.m.e, Fig. 11B) is developed near the posterolateral margin of the flange. Much of the flange lies well below the level of the space occupied by the brain. The posterior process did not contact the quadrate

and lies ventral and medial to the crista parotica (Fig. 3) without contacting it. The same condition is developed in both *Bienotherium* (Hopson, 1964: 7) and *Tritylodon* (SAM K405). The epipterygoid has a distinct sutural contact medially with the basipterygoid process of the basisphenoid (Fig. 11A).

*Periotic.* The opisthotic and prootic are fused to form a periotic as in *Oligokyphus* (Kühne, 1956: 48).

The prootic (Pro, Fig. 3) has a relatively large lateral exposure in comparison to more primitive forms such as *Thrinaxodon* (Hopson, 1964: fig. 1) and *Cynognathus* (Broili and Schröder, 1934: fig. 4). Anteriorly, a small foramen for the exit of ramus maxillaris ( $V_2$ ) and, more ventrally, a large opening for the passage of ramus mandibularis ( $V_3$ ) of N. trigeminus are situated on the suture with the epipterygoid (q.v.). A similar arrangement was illustrated by Parrington (1946: fig. 7A) in cf. *Scalenodon* and by Broom (1911: pl. 46, fig. 1) in *Cynognathus* (but see Broili and Schröder, 1934: fig. 4). The anterodorsal portion of the prootic forms a thin sheet of bone (anterior lamina of authors; a.l.pro, Fig. 11B), which overlaps the ventrolateral part of the parietal posteriorly. It contacts the ascending process of the epipterygoid anteriorly. An important difference between *Kayentatherium* (MCZ 8811 and 8812) and *Bienotherium* (Hopson, 1964: 10) is the absence of the "ventrolateral flange" below the exit for  $V_3$  in the former.

Behind the exit for  $V_3$  the prootic is drawn out into a prominent, laterally and slightly posteriorly directed flange (l.l.a, Figs. 2, 3, 11B). This structure is almost vertically positioned and is identical with the posteroventral flange in other Tritylodontidae (Hopson, 1964: 12; lateral lamina of Kühne, 1956). It is pierced by a large foramen (f.l.a.l; Fig. 11), presumably the passage of V. capitis lateralis. A second, slightly smaller foramen is situated just lateral to the latter in MCZ 8812, much as in *Tritylodon* (SAM K405). The pos-

teroventral flange enclosed the pterygoparoccipital foramen anteriorly but apparently not laterally. In MCZ 8811, a small foramen is located in the prootic just behind the medial recess for the semilunar ganglion (f.v, Fig. 11); a remark by Kermack *et al.* (1981: 92) to the contrary notwithstanding, it probably represents the exit for V. cerebri lateralis, which drains into V. capitis lateralis. A similar foramen has been observed in *Bienotherium* (Hopson, 1964: fig. 2) but MCZ 8812 lacks this feature and the vein presumably exited through the foramen for  $V_3$ .

The large cavum epiptericum lies medial to both the anterior portion of the prootic and the epipterygoid as in *Bienotherium* (Hopson, 1964: 14). Except for partial flooring by the parasphenoid alae, no floor is developed to the cavum, unlike the condition in *Morganucodon* and *Siniconodon* (Crompton and Sun, 1985: 109). The semilunar ganglion was housed in a fairly deep recess in the medial face of the prootic (MCZ 8811), which is bordered behind by a distinct semicircular rim. An enormous space ventrolateral to the brain is enclosed laterally by the quadrate ramus of the epipterygoid and the prootic and medially by the para-basisphenoid complex (Fig. 6). Posteriorly, this space served as a passage to a wide eustachian tube, as interpreted by Watson (1942: 104), and A. carotis interna and N. facialis traversed it. The pila antotica is ossified as a short process anteromedial to the hollow for the semilunar ganglion (MCZ 8812), much as in *Bienotherium* (Hopson, 1964: fig. 3, "P A"). As in *Bienotherium* (Hopson, 1964: 14), the prootic participates with the basisphenoid in the formation of the dorsum sellae (Fig. 11A).

The paroccipital process is short but massive. As in other Tritylodontidae (Ginsburg, 1962: fig. 11; Crompton, 1964: fig. 8; SAM K 405), it is much expanded anteroposteriorly and is divided by a ventral continuation of the squamosal sulcus into two distinct projections (Fig. 3). The anteroventral projection (a.p.pr) is bul-

bous and massive. Its lateral surface is devoid of perichondral bone. Hopson (1966: 443) and Kuhn (1971: 98) homologized this projection with the crista parotica in monotremes. Furthermore, Hopson noted a distinctly posteromedially curved process on the crista parotica in *Bienotherium* that appears to correspond to the hyoid process on the monotreme crista parotica. This feature is beautifully preserved in MCZ 8812 (p.hy.c, Fig. 3) and its distal extremity shows a distinct pit. The attachment of the stylohyal to the crista parotica in both monotremes and therians lies posterior to the external auditory meatus (Presley, personal communication). This was also the case in *Kayentatherium* (shy, Fig. 22) if the course of the external auditory meatus has been correctly restored. The posterodorsal projection of the paroccipital process also lacks a cover of perichondral bone laterally (p.p.pr, Fig. 3). It may be compared to the mammalian mastoid process and possibly served as the site of origin of a jaw-opening muscle. A shallow but extensive depression is located on the ventral aspect of the paroccipital process posteromedial to the crista parotica. Similar features in *Oligokyphus* (Kühne, 1956: 49) and *Tritylodon* (Ginsburg, 1962: fig. 11, "m.st.") have been interpreted by these authors as containing a stapedius muscle. It is equally plausible that this depression was occupied by *M. levator hyoidei* as in monotremes (Kermack *et al.*, 1981: 98).

The fenestra ovalis (f.ov) forms a deep pit, which is surrounded by a distinct bony rim (MCZ 8811; Fig. 11B) as in *Oligokyphus* (Kühne, 1956: fig. 13, "s"). The thick ventral portion of this rim was interpreted by Kühne to have been in contact with the stapedial foot-plate. Three foramina can be traced within the internal auditory meatus in MCZ 8811 and MCZ 8812. The anterior canal was for *N. facialis* (VII); a small foramen in its floor, right at the medial entrance into the meatus, opens into a canal that exits anteroventral to the fenestra ovalis in a foramen pro *N. faciali*

(VII, Fig. 11). The posterior canal is large and contained the ramus cochlearis of *N. acusticus* (VIII). The dorsal canal presumably carried the vestibular branch of VIII. An anteroposteriorly elongate foramen jugulare (for *V. jugularis interna*) is situated behind the fenestra ovalis.

The pterygo-paroccipital foramen (f.pt-p, Fig. 2) is large. *V. capitis posterior*, which drains the occipital musculature, probably passed forward through the posttemporal fossa to join *V. capitis lateralis* to form a common trunk. This trunk continued through the pterygo-paroccipital foramen to drain into *V. jugularis interna*. It is bordered by the posterolateral flange of the prootic anteriorly and by the crista parotica and squamosal posteriorly and medially. It is connected to the posttemporal foramen (f.p.t, Fig. 2) behind by a broad and shallow sulcus. A vascular canal enters the posttemporal fossa anteromedially (MCZ 8842); an identical canal in *Bienotherium* has been equated with the open groove ("sinus canal") in *Diademodon* (Watson, 1911) and other forms by Hopson (1964: 8). In some more primitive Tritylodontoidea (cf. *Scalenodon*; Parrington, 1946: fig. 7) the canal is already partially covered laterally by the prootic. Most authors believed that this canal contained an extracranial vein draining the orbital region; most recently, this vessel was homologized with *V. temporo-orbitalis* (Shindo, 1915) by Kermack *et al.* (1981: 91). But *V. temporo-orbitalis* extends *lateral* to the jaw musculature in embryonic *Lacerta* (Shindo, 1915: 412 and figs. 21–22) and, therefore, cannot be homologized with the feature in question in advanced synapsids. In *Oligokyphus* (Kühne, 1956: 49), a large foramen is developed in the fossa subarcuata, opening into a canal on the outside, strikingly similar to the condition in certain Multituberculata such as *Catopsalis* (Kielan-Jaworowska *et al.*, in press). No such foramen is developed in the relatively shallow fossa in *Kayentatherium* (MCZ 8812). Kielan-Jaworowska *et al.* (1984 and

in press) have argued that these canals or grooves contained arteries entering the region through the posttemporal fossa, perhaps similar to *A. diploetica magna* in *Tachyglossus*. While the evidence remains inconclusive, the possibility of primarily arterial affinities for the canal in tritylodontids discussed above seriously remains to be considered.

Just dorsal to the fossa subarcuata in *Oligokyphus*, a depression, misidentified as for the "lateral lobe of the cerebellum" by Kühne and Crompton, may be related to a venous sinus, possibly homologous to the mammalian sinus transversus (cf. *Ptilodus*; Simpson, 1937: fig. 8B, "S.T.S.").

*Basioccipital* (Bo). The basioccipital (Fig. 11) forms the posterior portion of the floor to the cavum cranii. Along its posterior margin between the occipital condyles it forms a shallow notch for the reception of the large dens (n.d., Fig. 11A). The dorsal surface of the basioccipital is transversely concave. Its ventral aspect bears a distinct, rounded median ridge, which separates the depressions for insertion of *M. rectus capitis anterior* (seu ventralis; d.m.r., Fig. 6). Extensive lateral facets for the exoccipitals are developed (MCZ 8811; art.eo., Fig. 11). The basioccipital becomes thicker anteriorly toward its sutural contact with the basisphenoid.

*Exoccipital*. The exoccipitals exclusively form the occipital condyles and presumably the lateral margins of the foramen magnum. Each is penetrated by a single, obliquely anteroventrally extending canal for *N. hypoglossus* (XII; MCZ 8839). Its dorsal extent cannot be determined on the available material.

*Tabular*. The tabular forms the dorso-lateral portion of the occipital plate, including much of the lambdoidal crest, and the dorsal margin of the posttemporal foramen on the occiput. Its posteroventral portion is clearly separated from the posterior paroccipital process by a groove on the occipital plate.

*Interparietal and supraoccipital*. Inadequate preservation of the available

specimens makes tracing of the sutural outlines of both bones impossible. A distinct median ridge in MCZ 8812, flanked by a depression on either side, presumably served as attachment for a well-developed ligamentum nuchae.

## LOWER JAW

*Dentary* (D). The dentary is the largest bone of the mandible and has a very tall coronoid process (co.p., Figs. 12, 13). The ventral margin is gently sigmoid behind the pronounced posteroventral part of the symphysis. As in *Bienotherium* (Hopson, 1966: fig. 3F) the mandibular symphysis (sy.m., Fig. 13B) is relatively shorter than that of *Oligokyphus* (Kühne, 1956: fig. 7B), and the incisor is less procumbent. The symphysis was not fused, and the symphyseal facet extends posteriorly to the level of the first lower postcanine tooth. A distinct but small angular process (an.p) is developed on the posteroventral angle of the dentary in MCZ 8811 (Fig. 13) but not in the very large specimen MCZ 8812 (Fig. 12). *Dinnebitodon* also has a small angular process (MNA V3222). Elsewhere, *Bienotherium* appears to have a prominent process on the angle (Young, 1947: fig. 5) but in *Oligokyphus* the posteroventral corner of the dentary forms almost a right angle (Kühne, 1956: fig. 7; Sues, 1985b: fig. 4A). Just above the angle there is a smoothly curving notch in the posterior margin of the dentary. The angle of the dentary bears distinct striations on the lateral aspect in MCZ 8812 (i.m., Fig. 12), here interpreted as the site of insertion for the superficial masseter muscle. The medial surface of the angle is flat and has a rough surface texture (MCZ 8811).

The coronoid process is very high, with a nearly vertical anterior margin in MCZ 8812 (Fig. 12) and a rounded dorsal border. In MCZ 8811 (Fig. 13), an immature specimen, the angle enclosed between a tangent to the anterior margin and the long axis of the dentary is 55°. The ascending ramus apparently became more

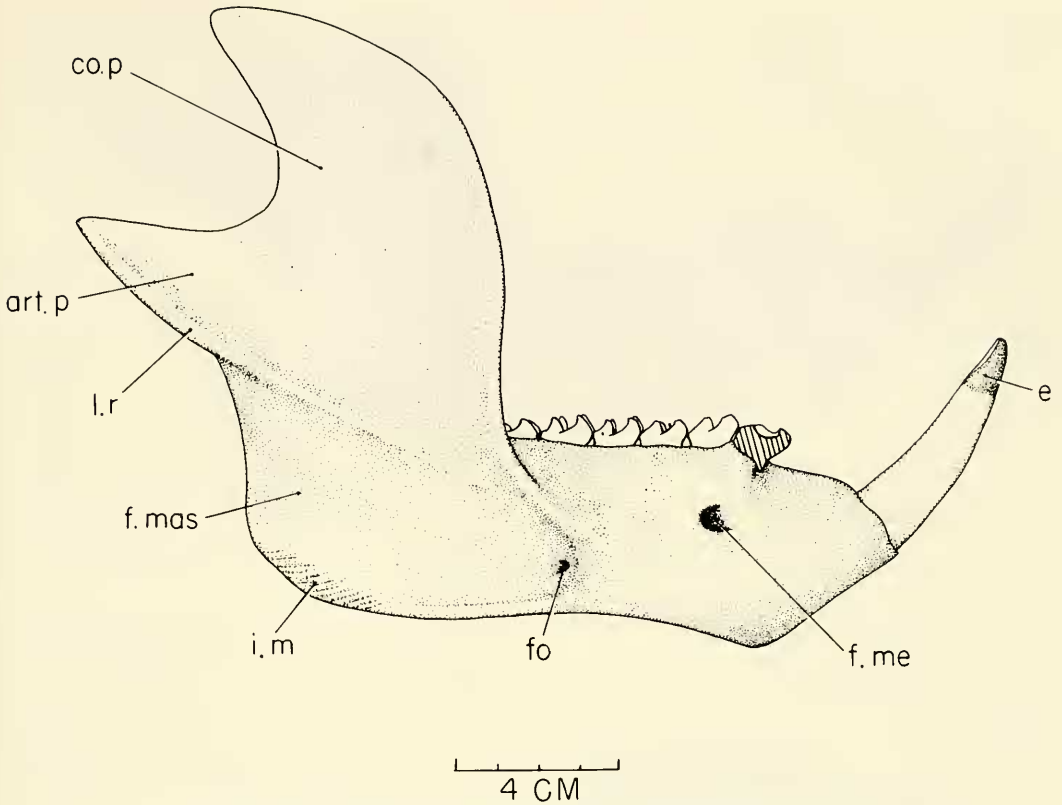


Figure 12. Right dentary of *Kayentatherium welllesi*, MCZ 8812. Lateral view.

upright during ontogeny, much as in mammals (e.g., *Homo*; Enlow, 1982: 148 and fig. 3-101). The anterior margin of the coronoid process forms a rounded ridge laterally, merging with the lateral surface of the tooth-bearing ramus of the dentary anteroventrally. The coronoid process is recurved posterodorsally to form a prominent hook (MCZ 8812), much as in *Tritylodon* (SAM K405) and "*Tritylodontoideus*" (Fourie, 1968: fig. 3A, "C.P."). The medial surface of the anteroventral portion of the ascending process is thickened to form a triangular buttress against which the coronoid bone is apposed (co.b, Fig. 14).

A well-developed masseteric fossa (f.mas) is developed on the posterolateral aspect of the dentary (Figs. 12, 13A). It is

divided by a rounded lateral ridge (l.r) that extends from about the center of the fossa to the articular process of the dentary where it becomes a narrow, flange-like projection. The ventral margin of the fossa is broadly rounded and wide in the region of the symphysis, becoming increasingly more narrow and less rounded posteriorly. A small foramen is occasionally developed near the anteroventral terminus of the masseteric fossa (MCZ 8812). A low lateral ridge is developed just anterior to the anterior end of the fossa in *Dinnebitodon*; it appears to be closely similar to a very distinct lateral shelf in this position on the dentary of *Bocatherium* (Clark and Hopson, 1985: fig. 1). A mental foramen (f.me) for exit of ramus mentalis of N. alveolaris inferior is situ-

ated below the anterior margin of the first lower postcanine tooth.

A single enlarged incisor is held in the collar-like alveolar process of the dentary in most specimens. It projects forward and upward. In one small, presumably juvenile specimen of *Dinnebitodon*, MCZ 8831, the base of a second, much smaller incisor is present. Older individuals of *Bienotherium* have also only a single lower incisor (Young, 1947: 451; Hopson, personal communication) whereas *Oligokyphus* may have up to three lower incisors (Kühne, 1956: fig. 7). A ridge (r.d) is developed between the incisor and the first lower postcanine tooth on the alveolar margin of the dentary.

The two mandibular rami diverge little posteriorly. As in *Oligokyphus*, the highest degree of divergence appears to occur in very small specimens such as MCZ 8839.

Corresponding to the lateral ridge on the coronoid process, there is a much more pronounced flange-like median ridge (m.r., Fig. 13B). As a result the articular process of the dentary (art.p) forms an inverted T in transverse section. The median ridge overhangs a wide, smoothly concave groove ("Meckelian sulcus" of Simpson; p.d.tr) for the reception of the postdentary bones. This sulcus extends from the mandibular foramen to the tapering posterior end of the articular process. The ventral limit to the groove is formed by an edge that extends from the mandibular foramen to the notch in the posterior margin of the dentary above the angle. The foramen mandibulare posterius (f.d) for *A. and N. alveolaris inferior* is large. Just anterior to the foramen, the internal groove (i.gr) commences, extending to the posterior end of the symphysis. This sulcus probably contained a persistent Meckelian cartilage, along with mylohyoid branches of *A. and N. alveolaris inferior*. It was at least partially covered by the splenial bone in life although the splenial is not preserved in any specimen. A division in the wall of the groove along much of its course can occasionally be observed, providing

further evidence for its double function as sulcus primordialis and sulcus mylohyoideus (Krebs, 1971: 93). On a few dentaries a distinct but short groove is located immediately behind the symphysis near the ventral margin of the dentary; it is apparently continuous with the internal groove posteriorly.

The lower postcanine tooth row twists behind the symphysis so that the more anterior teeth point laterally (at about 10°) and the more posterior teeth (especially the newly erupted ones) point medially (at about 20°) in MCZ 8811. The crowns of the more anterior postcanines also point increasingly forward. The twisting of the tooth row is particularly pronounced in immature specimens such as MCZ 8811. The dentary is recessed lateral to the tooth row more posteriorly.

*Coronoid (Co)*. The coronoid (Fig. 13B) is a more or less triangular bone located on the raised boss (co.b, Fig. 14B) on the medial aspect of the coronoid process of the dentary. Anteroventrally, it overlaps the medially expanded portion of the dentary that holds the posterior postcanine teeth. The lower half of the coronoid encloses a hollow (c.r.t) containing unerupted replacement teeth, much as in *Bienotherium* (Young, 1947: fig. 5). The anterior face of the coronoid is nearly vertical but its base is anteroventrally inclined. Two small foramina pierce the anterior aspect of the bone just above the level of the tooth row in MCZ 8811. The expanded base of the coronoid has a long posteroventral process that contacts the prearticular below and consists of very thin bone. It overlies the median ridge above the postdentary trough. The coronoid is especially thick posterodorsally. Its dorsal portion appears swollen and bears the same vermiculate texture that is developed on the pterygoid flange. The posterior face of the coronoid is deeply excavated in MCZ 8811 (Fig. 13B). The dorsal edge is rounded. When the mandible is occluded with the skull, the dorsomedial surface of the coronoid bone contacts the dorsolateral as-

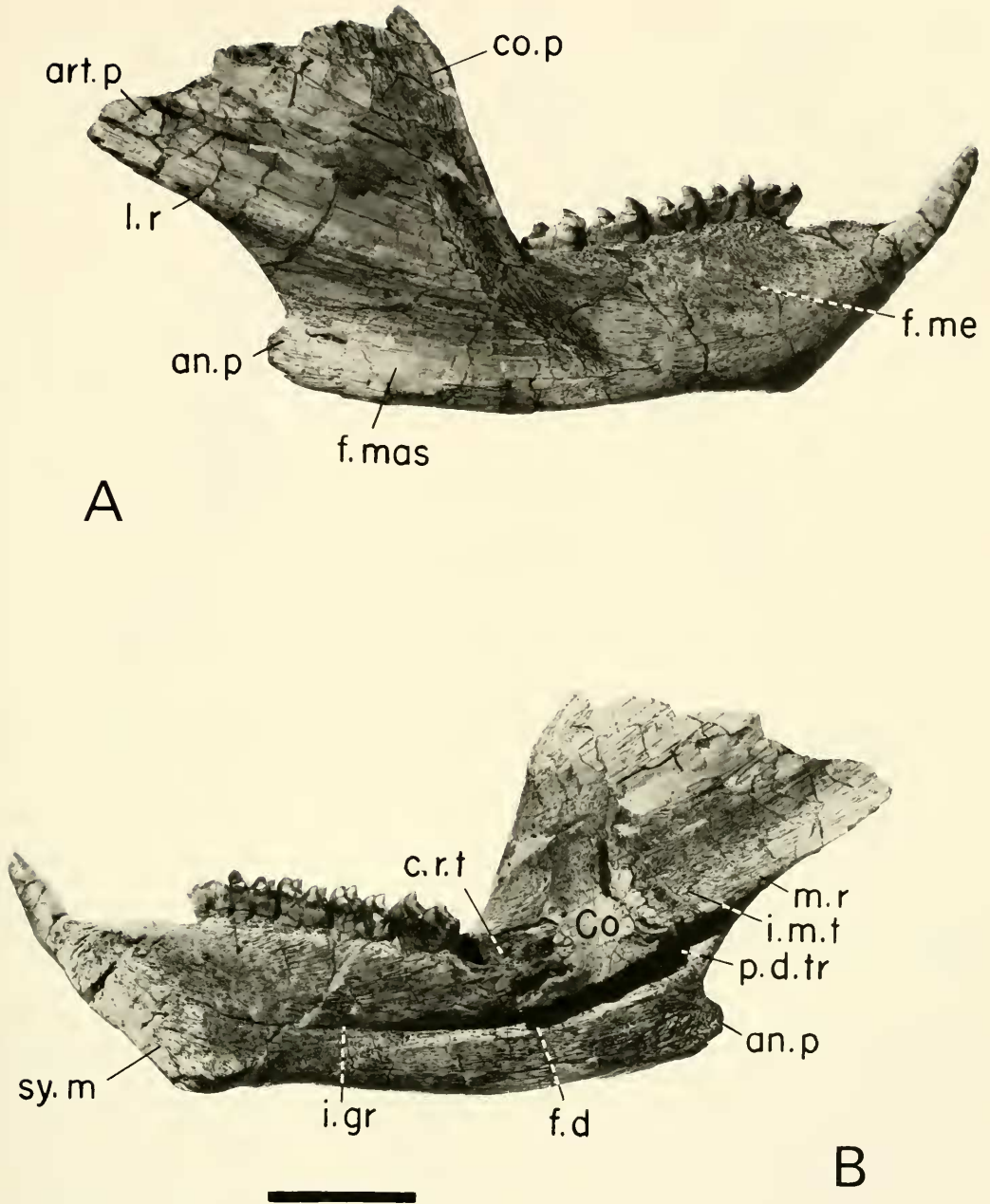


Figure 13. Right dentary of *Kayentatherium wellesi*, MCZ 8811. A) lateral view. B) medial view. Scale bar. 2 cm.

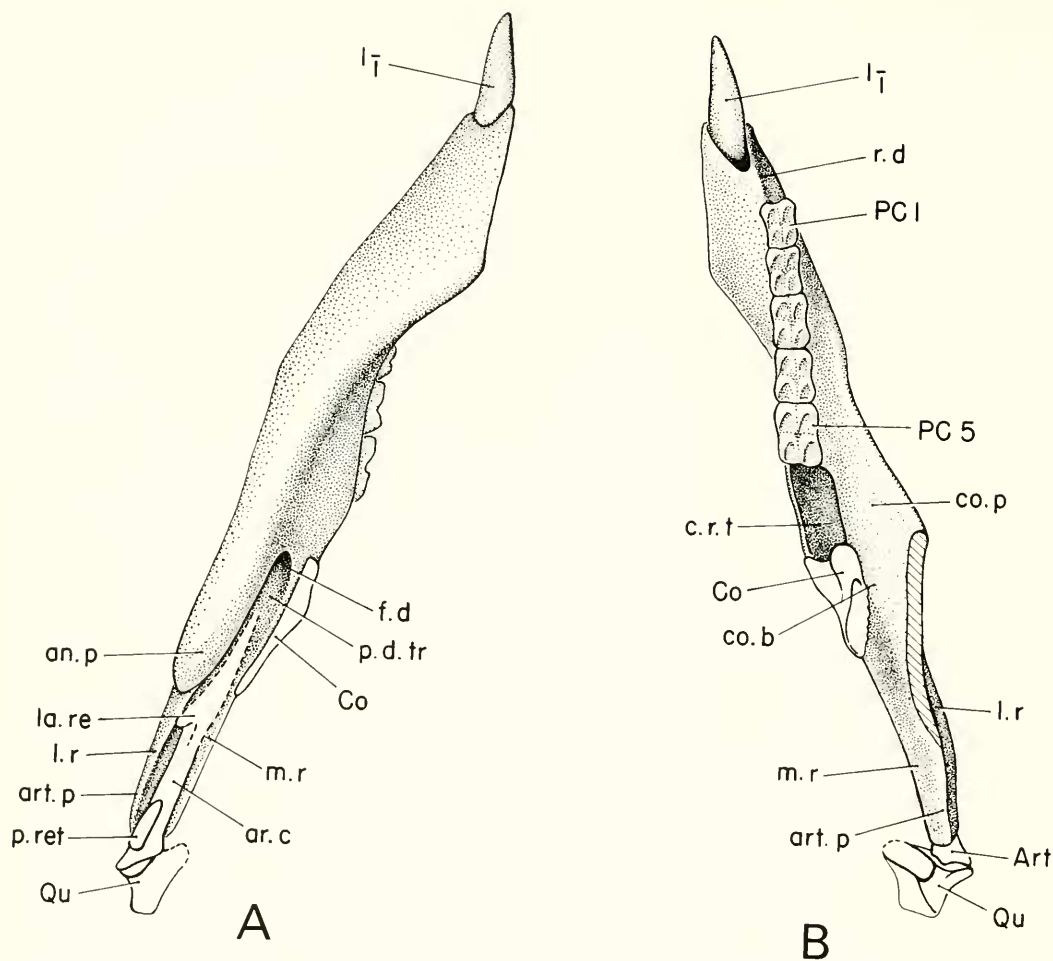


Figure 14. Lower jaw of *Kayentatherium wellsi*, MCZ 8811. Reconstruction in (A) ventral and (B) dorsal views. Hatching denotes broken coronoid process.

pect of the lateral flange of the pterygoid. This would have suppressed any significant transverse movements of the mandible (Watson, 1942: 108).

Kühne (1956: 34) claimed that *Oligokyphus* did not have a coronoid bone but the raised triangular contact of that element with the dentary is readily apparent and the coronoid has obviously been lost post-mortem. The mandible of the holotype of *Bienotherium yunnanense* Young, 1940 has this bone developed much as in *Kayentatherium* (Young, 1947: fig. 5).

*Articular and surangular (Art)*. The articular complex (Figs. 14–16) is composed

of the indistinguishably fused articular and surangular. The anterior portion of this complex forms a slender, tapering rod (ar.c) that was closely applied to the walls of the sulcus on the posteromedial aspect of the dentary. The lateral aspect of the articular rod is divided by a ridge into two surfaces, which are inclined on each other; the dorsolateral field contacts the dentary and the ventrolateral field the angular (MCZ 8811). A shallow depression extends along the medial surface.

The most prominent feature of the robust posterior portion of the articular complex is the large retroarticular process



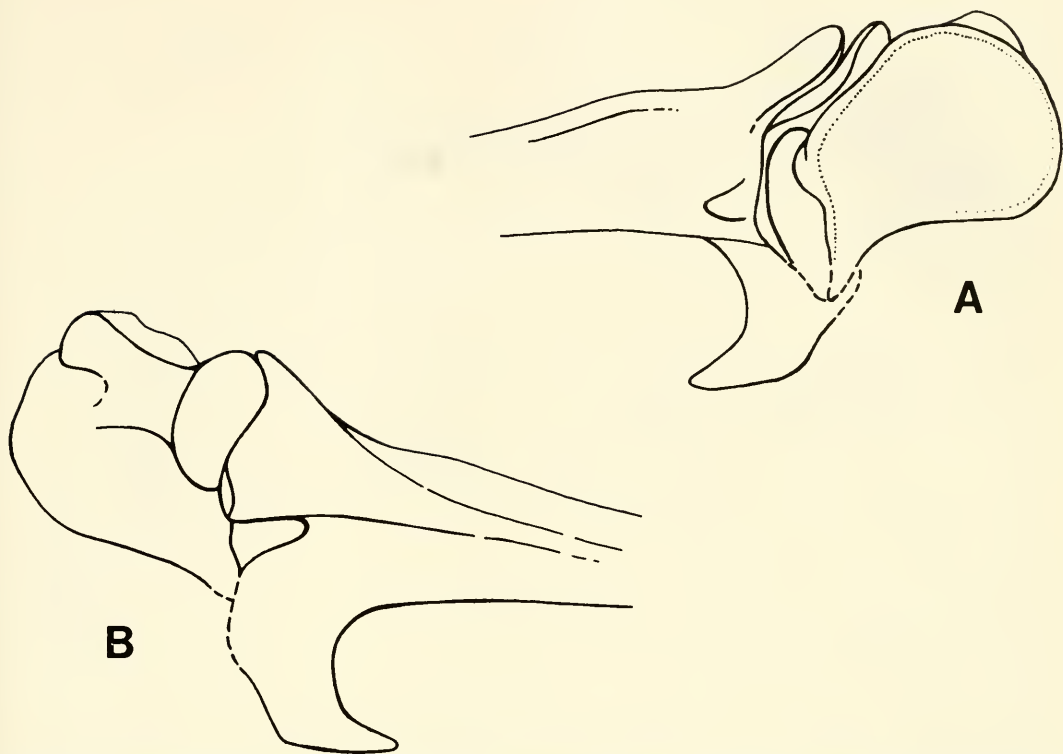


Figure 15. Articated right quadrate and articular of *Kayentatherium wellesi*, MCZ 8811. A) medial view. B) lateral view. Based on camera lucida sketches.

(p.ret, Fig. 16) with a forwardly directed "hook," which is closely similar to the manubrium mallei in monotremes (Hopson, 1966: fig. 8; Kuhn, 1971: fig. 4). The hook has a relatively thick posterior rim, apparently corresponding to the orbicular apophysis on the monotreme malleus (Fleischer, 1973: fig. 1), and is filled out by thin bone. The lateral surface faces anterolaterally and is concave dorsoventrally. The distal extremity of the retroarticular process is expanded and its ventral face is flat or gently concave. A foramen (fo.ch.t), probably for the chorda tympani (VII), is developed on the medial aspect of the base of the retroarticular process just below the articular facet for the quadrate trochlea. The chorda tympani would have had the same topographical position as in embryonic mammals (Fig. 23A).

The articular facet (art.f) for the quadrate trochlea forms a deeply concave

notch, which is partitioned into a small lateral and a larger medial facet. It is overhung by a distinct dorsal lip except for its medial portion. The notch is delimited ventrally by a pronounced horizontal ridge (when viewed from behind). This ridge appears to be drawn out into an acute posterior projection (d.p) in lateral view, much as in *Oligokyphus* (Kühne, 1956: fig. 8). The articular notch is open medially. The medial facet is more concave than the lateral one. The transverse axis of the articular notch is strongly inclined anteromedially (about 30° or 150° relative to the long axis of the articular rod (MCZ 8811). A blunt projection located just anteroventral to the articular notch (p.mus) is identical with a tubercle in *Oligokyphus* (Kühne, 1956: fig. 8B, "P.i.") and a rugosity in the same position on the articular in *Morganucodon* (Kermack *et al.*, 1981: fig. 88, "ten.ty.ar."). Kühne

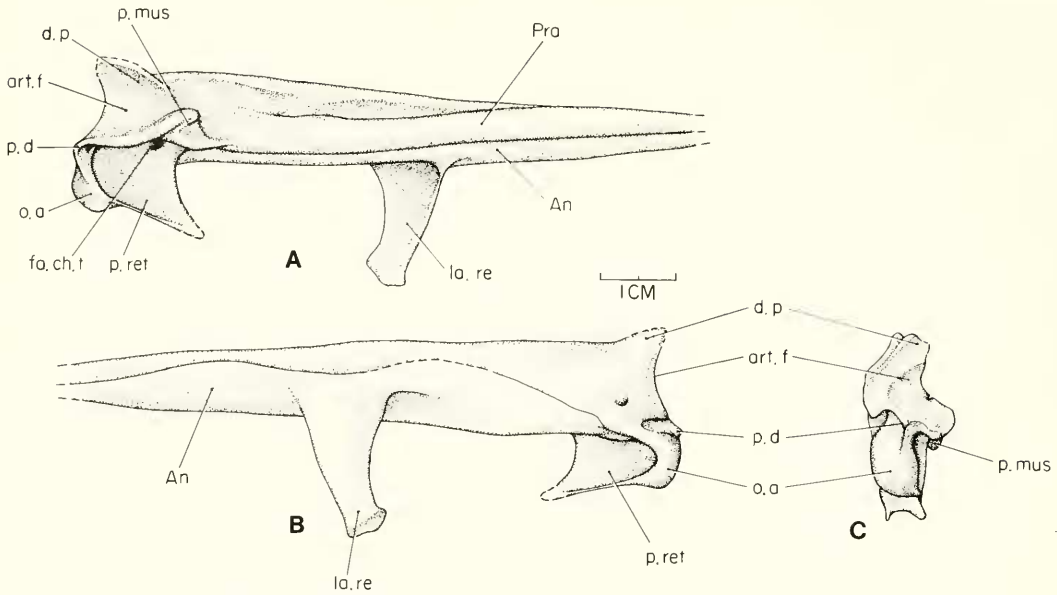


Figure 16. Left postdentary elements of *Kayentatherium wellsi*, MCZ 8812. A) medial view. B) lateral view. C) posterior view.

(1956: 38) has interpreted this feature in *Oligokyphus* as a processus muscularis for a muscle homologous to the mammalian *M. tensor tympani*.

The tritylodontid articular rod differs from those in *Cynognathus* (Kermack *et al.*, 1973: figs. 25, 26) and *Diademodon* (Kermack *et al.*, 1973: pl. 3, figs. F, G) especially in lacking the pronounced boss on the surangular for contact with the squamosal (incorrectly identified as the retroarticular process by Kermack *et al.*, 1973) and, furthermore, in the distinct anteromedial inclination of the articular facet.

**Prearticular (Pra).** The posterior sutural contact of the prearticular with the articular has been obliterated (Fig. 16A) but otherwise the bone is clearly distinct from the remainder of the articular complex. It forms a bony rod medial and slightly ventral to a median gap that is laterally enclosed by the surangular. The ventrolateral surface of the prearticular contacts the angular below.

**Angular (An).** The angular is situated ventral and lateral to the articular com-

plex (Fig. 16). Its posterior portion forms a thin dorsal flange and terminates just in front of the posterior end of the retroarticular process. It is fairly thick and overlaps the lateral aspect of the articular. More anteriorly, a large reflected lamina (*la.re*) emerges from the ventrolateral margin of the angular rod and extends posteroventrally. It is fairly wide anteroposteriorly and only slightly curved backward. The medial surface of the broad proximal base of the lamina is excavated. Anterior to the reflected lamina the angular continues as a tapering rod (MCZ 8812, MNA V3141).

#### HYOID APPARATUS

A number of disarticulated elements found in the matrix behind the dentaries of MCZ 8812 are clearly referable to the hyoid apparatus. Virtually nothing has been reported in the literature about this feature in non-mammalian synapsids. A few hyoid bones are known in dicynodonts (Cluver, 1971), and caseid pelycosaurs have a well-developed hyoid apparatus (Olson, 1968: 246; Sigogneau-Russell

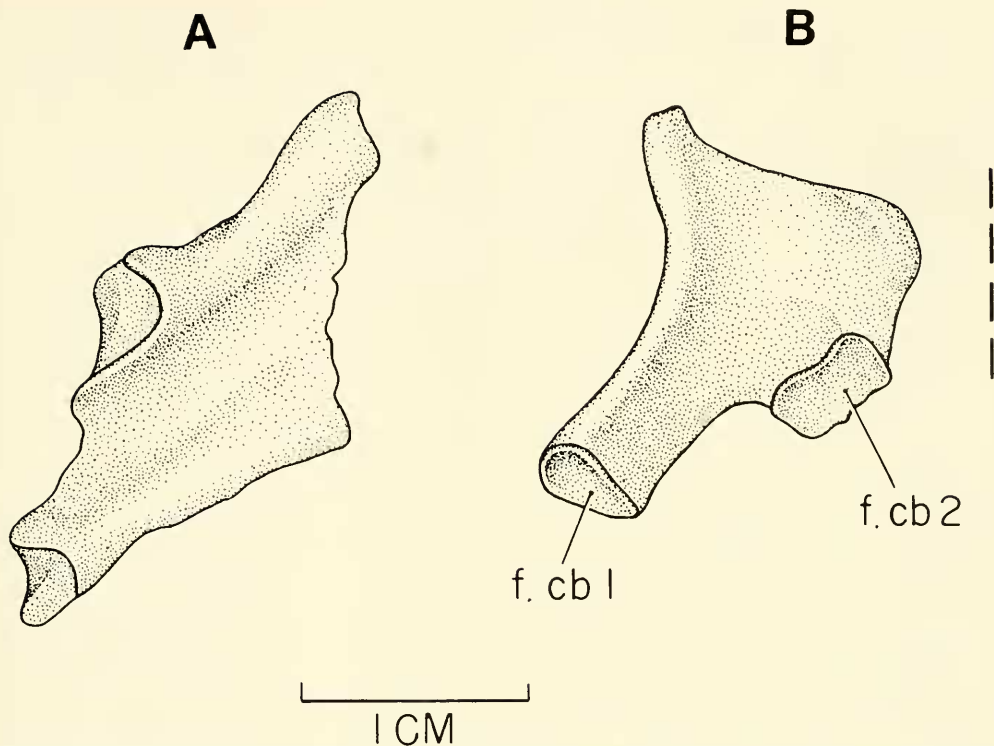


Figure 17. Hyoid elements of *Kayentatherium wellesi*, MCZ 8812. A) element from the (?) second branchial arch. B) basihyal element. Broken line indicates inferred midline.

and Russell, 1974: fig. 13). Rod-like hyoid elements are not uncommon in the galesaurids *Galesaurus* and *Thrinaxodon* (Hopson, personal communication). Identification of the slightly distorted elements in MCZ 8812 is difficult owing to the lack of extant analogues. They appear to be most similar in shape to the hyoid elements in modern turtles (Gaupp, 1905: figs. 38–40).

The first type of element, represented by bones from opposite sides, may reasonably be interpreted as a copula hyoidei. Fusion of the copulae in mammals produces the basihyal. The element (Fig. 17B) bears a prominent posterolateral process with a terminal facet (f.cb 1) and, posteromedially, a distinctly off-set second facet (f.cb 2). If it is indeed a copula, these cup-shaped facets presumably were for articulation with elements of the branchi-

al arches 1 and 2, respectively, based on the condition in living amniotes (Gaupp, 1905). The dorsal surface of the median plate is thin and transversely concave. The bone forms a short anterolateral process, possibly for contact with a ceratohyal.

A second type of hyoidal element is an elongate, curved rod. It bears a cup-shaped facet at one end and is flattened at the other. It almost certainly represents a first ceratobranchial. There is also a shorter, straight bony rod with obliquely inclined facets at either end.

A fourth type of hyoidal element is represented by a thin rhomboidal bone. It bears two facets at one end and a smaller terminal one at the other end (Fig. 17A). One of its surfaces is distinctly concave transversely. I have not found any comparable element in another tetrapod. The bone in question may represent a segment

of the second branchial arch, homologous to the mammalian cartilaginous thyroidea.

## DENTITION

*Upper incisors.* Both immature and adult specimens of *Kayentatherium* have but a single incisor in each premaxilla. This deeply rooted tooth is greatly enlarged, robust, and often recurved. It corresponds to the second upper incisor in *Dinnebitodon* and other Tritylodontidae. The enamel covering is very thin and apparently restricted to the apical portion of the crown. The long root forms an anteroposteriorly elongate oval in transverse section. A very extensive lingual wear facet was formed by contact with the buccal edge of the enlarged lower incisor. As in *Oligokyphus* (Kühne, 1956: 87), the corresponding wear on the lower incisor is extraordinarily slight. Deep oblique grooves have been cut by the lower incisors into the lingual faces of the enlarged second upper incisors in one specimen referable to *Dinnebitodon* (MCZ 8836). Although it is poorly defined in MCZ 8812, a second facet cuts away the anterior aspect of the tip of the upper incisor (Fig. 8).

*Lower incisors.* Typically a single enlarged lower incisor is held in each dentary in both *Dinnebitodon* and *Kayentatherium*. A second, much smaller incisor is developed only in one specimen of *Dinnebitodon* (MCZ 8831). The tusk-like lower incisor is distinctly procumbent and converges distally to meet its fellow (MCZ 8812; Fig. 8). The thin covering of enamel appears to be restricted to the anterobuccal aspect of the tip of the crown. The cutting edges are sharp. The lingual aspect of the apical region is flat and the posterior face is gently concave.

*Upper postcanine teeth.* The quadrangular crown of each upper cheek-tooth is divided into three anteroposterior rows of cusps by two longitudinal furrows (Figs. 18A, 19A). It is (buccolingually) wider than long. The ratio of crown width to crown length, measured on a sample of undistorted teeth, ranges from 1.04 to 1.14

and is comparable to that of most other Tritylodontidae except *Oligokyphus*. D. M. Kermack's (1982) comment to the contrary notwithstanding.

The cusps of the median row are symmetrically crescentic but those of the buccal and lingual rows are variously asymmetrically so. All crescents open forward and are buccolingually compressed. The buccal row is always shorter than the other two rows and has only two principal cusps. The medial wing on the anterior cusp extends further anteriorly than does the lateral one. The large posterior cusp, the tallest one on the entire tooth, sends a distinct posteromedial crest that extends into the groove and is more prominent than the lateral one. The median row has three cusps, which increase in size from front to back. The wings of the second cusp envelop much of the preceding cusp, which is distinctly smaller and often has an irregular, wrinkled face (MCZ 8842). Its small size led D. M. Kermack (1982) to call it an accessory cusp; however, this term is only meaningful when it is also applied to the equally small anteromedian cusp in other Tritylodontidae such as *Tritylodon*. Two crests extend from the apex of the very large posteromedian cusp to the posterior ends of the outer and inner furrows, respectively. They form posterior cingula together with ridges from the posterobuccal and posterolingual cusps, respectively.

The upper cheek-teeth of *Dinnebitodon amarali* have two asymmetrically crescentic lingual cusps, the anterior one of which is smaller than the posterior one (Sues, 1986a; Fig. 20). The posterolingual cusp sends a crest from its apex to the posterior end of the inner furrow. *Kayentatherium wellesi* has upper postcanine teeth with three lingual cusps (Fig. 18A). D. M. Kermack's (1982: 7) report of only two lingual cusps is based on the inadequately preserved and prepared type-specimen, and slight additional cleaning of the ultimate cheek-tooth in the left maxilla revealed the same configuration as described here (Sues, 1986b). The an-

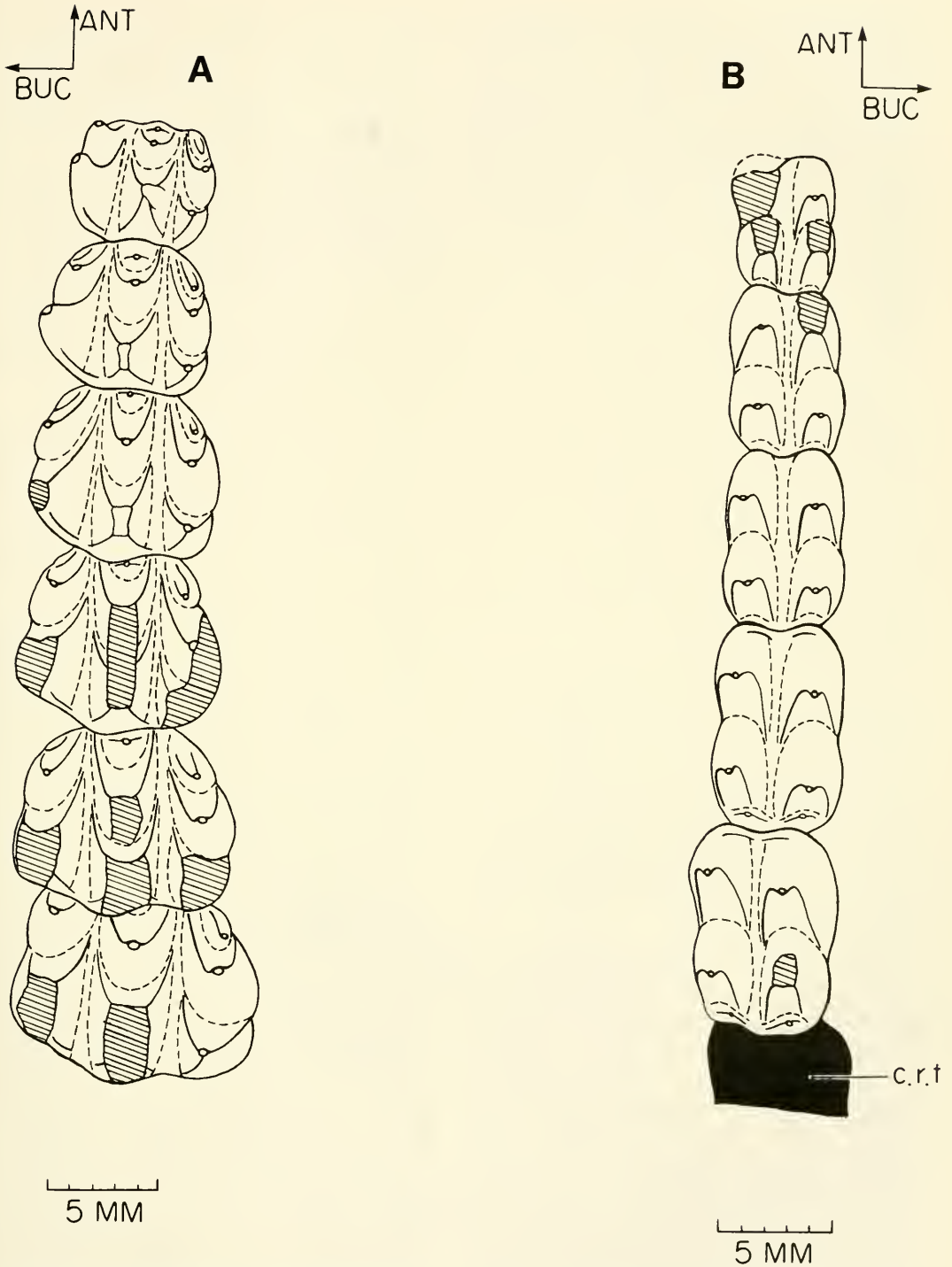


Figure 18. Postcanine dentition of *Kayentatherium wellsi*, MCZ 8811. A) right maxillary tooth row. B) right dentary tooth row. Occlusal views. Hatching denotes broken or damaged cusps.

termost lingual cusp is the smallest and often forms a mere ridge, extending obliquely to the anterior terminus of the inner furrow. It is completely embraced buccally by the wing of the large, distinctly asymmetrical second cusp. The latter cusp sends a posteromedial ridge to the lingual margin of the crown. The posteriormost cusp is smaller than its predecessor and its anterior face is less asymmetrical. It has a triangular outline in occlusal view and sends a distinct crest to the posterior terminus of the inner furrow.

Accessory cuspules are present on newly erupted and moderately worn teeth of both *Dinnebitodon* and *Kayentatherium*, especially near the anterior end of the buccal row of cusps (Figs. 18A, 20). These cuspules form distinct swellings on the lateral wing of the anterobuccal cusp and the medial wing of the anterolingual cusp. In some cases they are delimited by mere nicks in these crests. Butler (1939: 516) has noted similar cuspules on upper postcanine teeth in *Tritylodon*.

Two fairly slender posterior roots are arranged in a transverse row. Anteriorly, three roots are joined immediately below the level of the crown into a single transverse structure but they are distinct within the alveoli. The median root is the largest and projects well in front of the anterior margin of the extraalveolar portion of the tooth as in *Tritylodon* (Simpson, 1928: 17) and fits tightly against the posterior face of the preceding tooth.

*Lower postcanine teeth.* The crown of each lower cheek-tooth is divided into two anteroposterior rows of cusps by a deep longitudinal groove (Figs. 18B, 19B). It is always longer than wide. Each row has two principal, symmetrically crescentic cusps. The crescents open backwards. The anterior cusp in each row is larger than the posterior one. A distinct cuspule is situated on the concave posterior face of each posterior principal cusp; these cuspules are also apparent in D. M. Kermack's illustrations (1982: figs. 8B, 9B) even though that author denies their existence. A ridge-like accessory cuspule is also developed on the

convex anterior aspect of the tall anterior cusps.

The teeth have two transverse roots. The anterior root has approximately a figure-eight shape in transverse section and the posterior root is more rounded.

*Ontogenetic changes in the dentition.* The available sample of complete or nearly complete dentitions for both *Dinnebitodon* and *Kayentatherium* is small. Metrical comparisons of the teeth are frequently not feasible because of fracturing and distortion of the tooth crowns. Therefore, only some qualitative remarks about the mode of tooth replacement can be made at present.

Replacement of the upper incisors appears to be restricted to smaller, immature specimens in both *Kayentatherium* and *Dinnebitodon*. One specimen of the former, MCZ 8811, with an estimated skull length of about 13.5 cm (measured along ventral aspect), shows erupting teeth in crypts just posteromedial to the upper incisor (Pr, Fig. 6). Larger individuals of this genus such as MCZ 8812, with a skull length of about 26 cm, and MNA V3141 do not display replacement of incisors. One small specimen of *Dinnebitodon* (MCZ 8830) has an erupting incisor posteromedial to the right second upper incisor whereas the larger MNA V3222, the holotype of *D. amarali*, again shows no incisor replacement.

The number of postcanine teeth increases slightly during ontogeny. Teeth are lost in front and new teeth are added at the posterior end of the tooth row as the jaw grows, much as in other *Tritylodontoides* (Crompton, 1955: 649). The number of postcanine teeth in the Mid-Triassic tritylodontoid *Scalenodon* increases from five in the smallest known specimen to eleven in the largest (Crompton, 1955: fig. 12). The number of postcanines in the upper and lower jaws of *Kayentatherium* increases from five (USNM 317203 and UCMP 83671) to seven (MCZ 8812). In *Dinnebitodon*, it increases from four (MCZ 8830) to five (MNA V3222). (The discovery of further ontogenetic stages

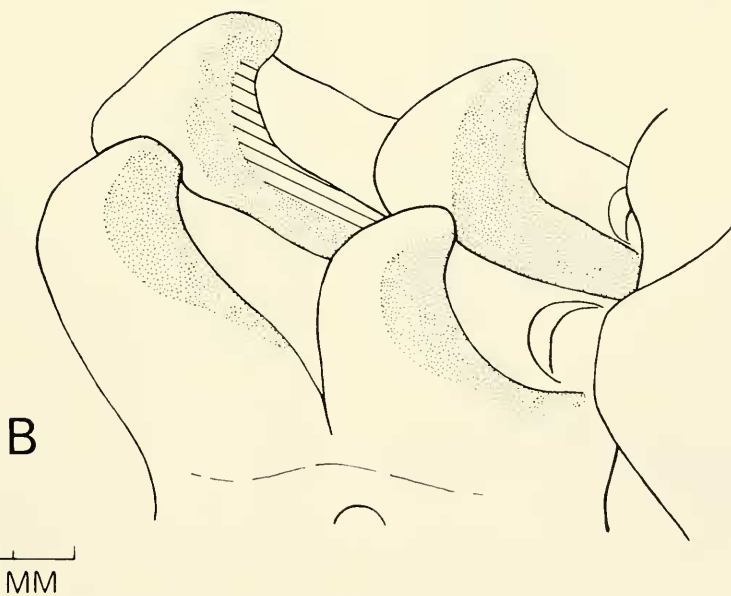
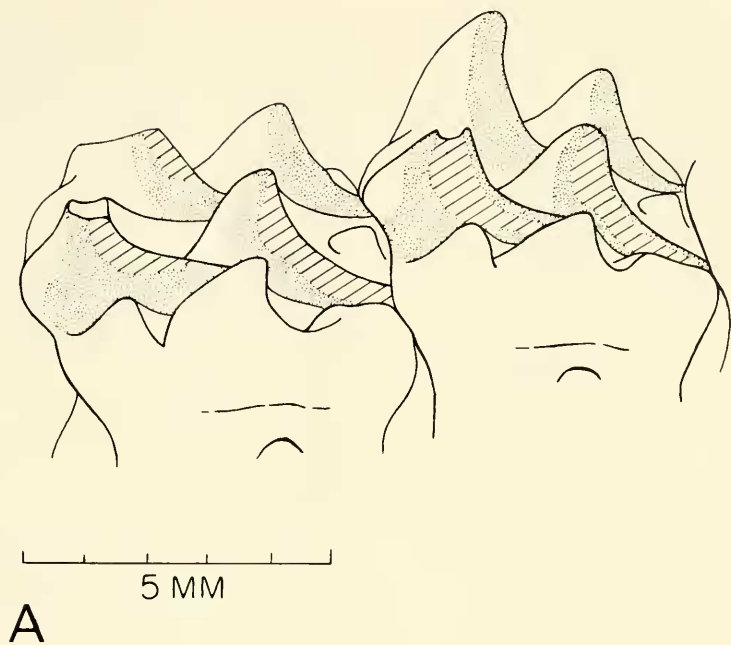


Figure 19. Wear on the right first and second upper postcanines (A) and on the right fourth lower postcanine (B) of *Kayentatherium wellesi*. Stippling indicates wear on the enamel, oblique hatching exposed dentine.

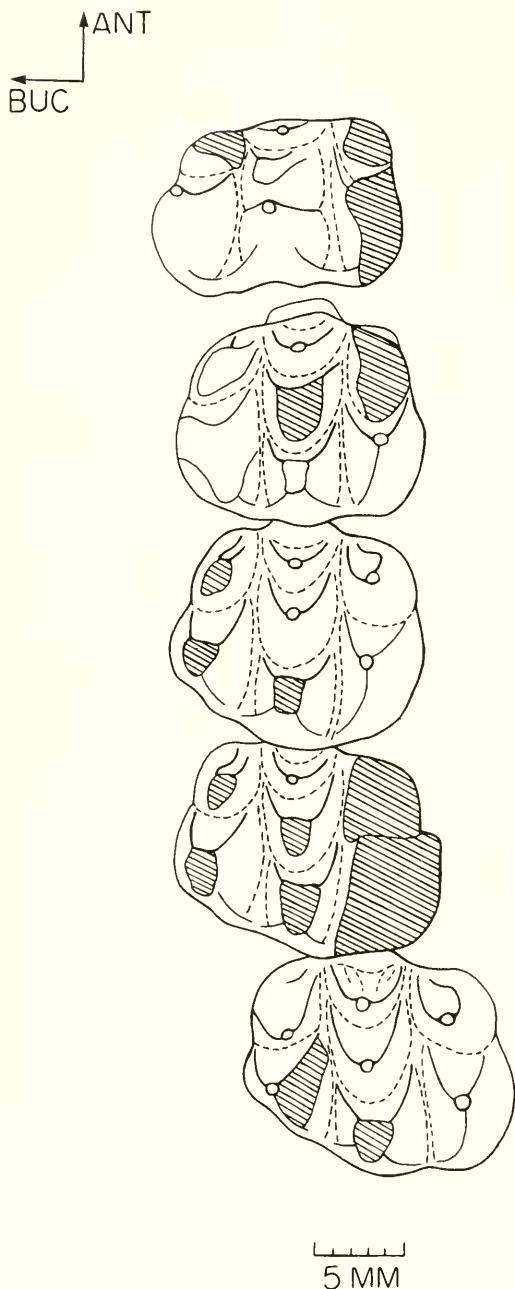


Figure 20. Right maxillary tooth row of *Dinnebitodon amarali*, MNA V3222 (holotype), in occlusal view. Hatching denotes damaged areas.

may, of course, further increase these ranges.) The posteriormost cheek-tooth is never fully erupted. The buccolingual width of the postcanine teeth increases progressively in immature specimens (MCZ 8811) but in the largest known individuals (MCZ 8812) the posterior teeth begin to decrease in width. A similar ontogenetic change has also been observed in *Bienotherium* (Young, 1947: 553) and *Oligokyphus* (Kühne, 1956: 76) as well as in more primitive Tritylodontoidea such as *Scalenodon* (Crompton, 1955: 651).

As noted previously, new teeth were added at the back of the tooth row while teeth were lost in front. Toward the anterior end of the tooth row in MCZ 8811 and 8812, the roots of the cheek-teeth become progressively more exposed through resorption of the surrounding alveolar bone. In none of the currently available specimens did I observe an empty alveolus anterior to the first functional postcanine tooth but such alveoli do occur in *Oligokyphus* (Kühne, 1956: pl. 2, fig. 3). Apparently the tooth was shed with its roots virtually intact and then the alveolus was very quickly filled with bone (Kühne, 1956: 69). This loss of anterior teeth partially contributed to an ontogenetic increase in the relative length of the diastema. New lower postcanine teeth were formed in a posterior extension of the tooth-bearing part of the dentary medial to the coronoid process (c.r.t., Fig. 13B). The bone surrounding the new teeth was thin, much as that around the replacement teeth in the maxilla. The crowns of newly erupted lower postcanines initially are inclined lingually (MCZ 8837) but they increasingly turn buccally and anteriorly further forward along the tooth row. The postcanine teeth also become more tightly appressed against one another anteriorly.

#### JAW MUSCULATURE

Crompton (1963) and Barghusen (1968) both have attempted detailed reconstructions of the adductor jaw musculature in advanced non-mammalian synsids.



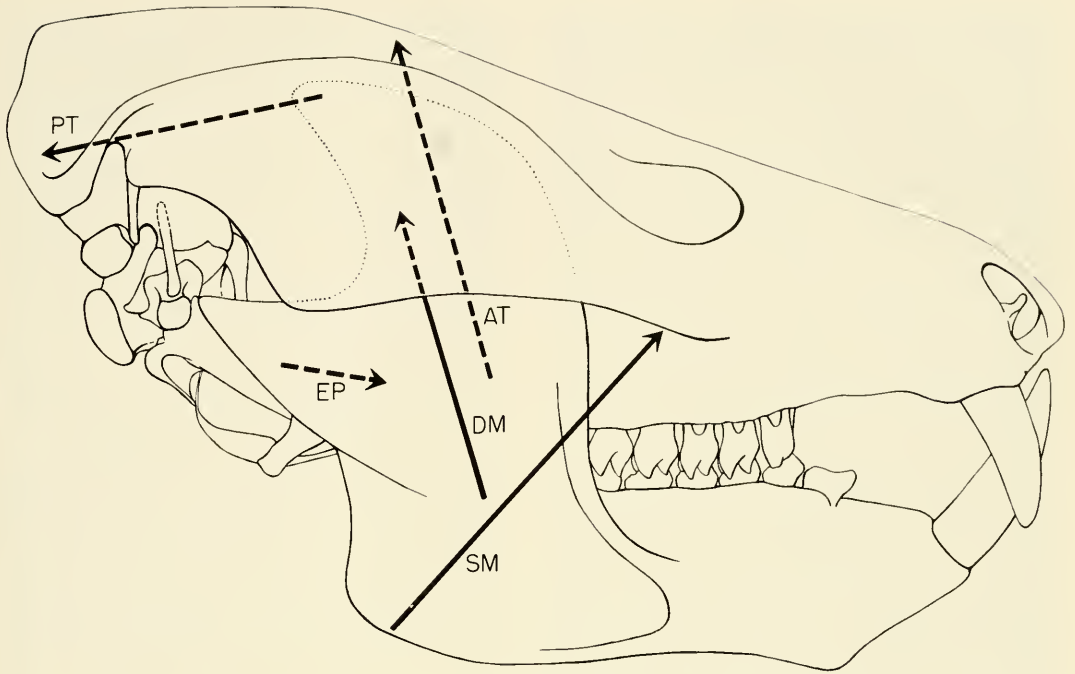


Figure 21. Diagrammatic reconstruction of the action lines for the adductor jaw muscles in *Kayentatherium wellsi*. Skull outline from MCZ 8812. Right lateral view.

Their considerations form the foundation for the following interpretation of the origins and insertions of these muscles in *Kayentatherium* (Fig. 21).

*M. masseter*. The masseteric fossa on the dentary is very large and is continuous over the entire lateral surface of the ascending ramus of the dentary. It is partially divided by a lateral ridge (masseteric ridge of Kühne, 1956) into a larger dorsal portion on the prominent coronoid process and a smaller ventral portion. The lateral and medial ridges on the ascending ramus have been interpreted by Crompton (1963: 719) as structural reinforcements against bending and shearing forces related to muscular contraction. A distinct change in surface topography occurs at the anterior terminus of the masseteric fossa from the floor of the fossa to the convex lateral aspect of the tooth-bearing portion of the dentary, much as on mammalian mandibles.

The deep masseter (pars profundus, DM) presumably inserted on the lateral surface of the coronoid process and formed a major component of the masseter complex. The superficial masseter (pars superficialis, SM) probably arose from the ventral aspect of the anterior root of the zygoma whereas the pars profundus arose along the medial face and the ventral margin of the deep zygoma behind the orbit. The anterior zygomatic root bears a prominent ventral ridge below the orbit. The peculiar articulation between the jugal and maxilla in the *Tritylodontidae*, well-illustrated in *Oligokyphus* by Kühne (1956: fig. 6), suggests considerable tensile forces produced by a posteroventrally pulling superficial masseter with a concentrated tendinous attachment. A comparable tenon-and-mortise sutural pattern has been noted in extant suids by Herring (1972: fig. 8). The long oblique suture between the jugal and squamosal may be

correlated with the action of the deep masseter extending more or less perpendicular to it. The superficial masseter inserted on the angle of the dentary as is attested by distinct striations along the ventrolateral margin of the angle in MCZ 8812 (i.m, Fig. 12). Therefore, I consider the angle of the tritylodontid dentary homologous to the angular process in the-rian mammals, contrary to a recent suggestion by Jenkins *et al.* (1983: 1234) that this process in non-mammalian synapsids and non-therian mammals should be called a pseudangular process, as first suggested by Patterson and Olson (1961). I believe that the "pseudangular process" in *Dinnetherium* (Jenkins *et al.*, 1983: fig. 1f-g) is actually homologous with the angle of the therian dentary and that the "angular process" is autapomorphous. It is apparent from examination of MCZ 20870, a well-preserved right dentary of *Dinnetherium*, that the "angular process" is produced by downward growth of the lateral ridge of the articular process. "Fusion" of this process with the "pseudangular process" could have produced the condition in the Multituberculata, Symmetrodonta, and Triconodonta (Simpson, 1928: figs. 9, 19) where the ventral margin of the dentary is continuous from symphysis to condyle. Pars superficialis of *M. masseter* in tritylodontids had an anterodorsal orientation of its fibers, presumably close to the vertical plane, whereas pars profundus (seu zygomatico-mandibularis) must have had a more posterodorsal course of its fibers.

*M. temporalis*. The well-developed sagittal and lambdoidal crests defining the perimeter of the temporal fossa provide suggestive evidence for the presence of a temporal aponeurosis that superficially covered the fossa (Barghusen, 1968: 27). Aside from serving as an area of origin for part of *M. temporalis*, this fascia probably also aided the zygomatic arch in resisting tensile forces produced by *M. masseter*, as has been experimentally demonstrated in mammals by Eisenberg and Brodie (1965).

As in mammals, most of the posterior

temporalis fibers (PT) probably originated from the expanded posterodorsal portion of the temporal fossa, the sagittal and lambdoidal crests, and the overlying temporal fascia. The main axis of the muscle extended in a nearly horizontal plane. Its fibers must have exercised a strong posteriorly to posteromedially directed pull in the direction of the posterior V-shaped notch in the squamosal. The distinctly hook-shaped posterodorsal extremity of the coronoid process presumably formed within the joint tendinous insertion of the posterior temporalis fibers. The anterior temporalis (AT) probably originated from the well-ossified lateral wall of the braincase, especially from the extensive area behind the orbital fissure. It apparently broadly inserted on the medial aspect of the ascending ramus of the dentary above the medial ridge. A distinct pocket is formed by the excavated posterior face of the coronoid bone and the adjacent surface of the dentary (MCZ 8811; i.m.t, Fig. 13B). As restored, the fibers of the anterior temporalis have a posterodorsal orientation.

*M. pterygoideus*. A tubercle on the medial aspect of the articular complex anteromedial to the facet for the quadrate trochlea has been interpreted by Kühne (1956: 38) as the site of insertion for a slip of the medial (internal) pterygoideus muscle, which is presumably homologous to the mammalian *M. tensor tympani*. This muscle might have originated from the distinct posterolateral flange along the posterior ramus of the pterygoid. Crompton (1963: fig. 7, "i.i.p.") believed that an internal pterygoideus inserted on the medial face of the angle of the dentary. Bramble (1978: 294) has rejected that suggestion and instead suggested that a digastric-like muscle inserted at that site; I am not convinced by the arguments in support of his reconstruction.

The existence of a lateral (external) pterygoideus muscle (EP) can be hypothesized on functional grounds. None of the previously discussed jaw muscles has a sig-

nificant protractive vector component. A possible site of insertion is the smooth medial surface of the articular process of the dentary, as first indicated by Crompton (1963: fig. 7, "i.e.p.").

No direct osteological evidence exists for the presence of a depressor mandibulae muscle, which was inferred by Allin (1975). There is no trace of such a muscle during the ontogenetic development of modern mammals (Presley, 1984: 187), and *M. depressor mandibulae* may well prove to be a uniquely sauropsid feature. Jaw opening in both primitive and advanced synsids could have simply been accomplished by hyoid muscles, and *M. digastricus* may only occur in therian mammals. Experimental evidence suggests that *M. detrahens*, long considered the monotreme equivalent of the therian digastric muscle, is not involved in jaw-opening in at least *Tachyglossus* (Crompton, personal communication).

#### FUNCTIONAL CRANIOLOGY

The masticatory apparatus of tritylodontid synsids has undergone considerable structural modification relative to that in related non-mammalian synsids. Recent experimental studies on mammalian mastication provide a framework within which certain features of the tritylodontid skull and dentition can be interpreted in functional terms.

*Masticatory apparatus.* The much enlarged incisors were clearly not adapted for gnawing or substantial incisive biting. The amount of wear, especially on the procumbent lower incisors, is surprisingly small. They probably served in seizing and holding plant material that then was torn off its substrate mainly by the power of the neck musculature, as commonly in mammalian herbivores (Weijs and Dantuma, 1975: 23). This would have limited the amount of bite force necessary and is consistent with other inferences concerning the function of the jaw joint. The well-developed tongue (judging from the hyoid skeleton and the well-developed diaste-

ma) probably aided in the gathering and, along with muscular cheeks (inferred from the arrangement of the maxillofacial foramina and from the inset tooth rows), in subsequent oral manipulation of the food. The wear facet on the anterior aspect of the tip of the enlarged upper incisor appears to be the result of contact with the substrate during rooting or other foraging activities.

During occlusion of the upper and lower postcanine teeth, the two rows of lower cusps fit between the three rows of upper cusps. Wear facets are developed on the sides of all cusps (Fig. 19) except for the buccal sides of the buccal cusps and the lingual sides of the lingual cusps on the upper teeth. These attritional facets are oriented nearly vertically and have a polished appearance. Examination at higher magnification, however, reveals the presence of parallel sets of anteroposteriorly extending microstriae, which indicate unidirectional, horizontal jaw movements. The anterior crests of the upper cusps and the posterior crests of the lower cusps can be viewed as a multiple cutting mechanism (Crompton, 1972: 61). In rodents such as *Rattus* the mandible is drawn forward during mastication; the crests on the upper molars are concave posteriorly and those on the lower teeth concave anteriorly (Rensberger, 1973: 522). As the reciprocally concave leading cutting edges meet, they enclose an ovoid space, the size of which progressively decreases during dynamic occlusion. This reversal of curvature in occluding teeth limits the area of tooth-to-tooth contact and maximizes occlusal pressure at the contacts at any given instant in time. Because the curves are usually concave in the direction of relative motion a posteriorly directed movement of the mandible can be inferred for tritylodontids, much as in multituberculates (Krause, 1982: 273). During dynamic occlusion, a lower tooth initially makes contact with an upper tooth one position further anteriorly and then, during mandibular retraction, the lower tooth comes

into occlusal contact with a second upper tooth (Crompton, 1972: fig. 13L). Because of the complex nature of the occlusal plane, produced by differences in axial tilting of the individual teeth along the jaws (see above), the postcanine teeth did not occlude simultaneously. This would have increased the bite force across individual teeth as they sequentially came into occlusion. Significant transverse movements of the mandible would have been suppressed by the occlusal relationships of the greatly enlarged incisors and of the postcanine teeth as well as by the contact with the robust lateral flanges of the pterygoid. The commonly observed apical pitting on the cusps can be related to the initial puncture-crushing action when the food bolus was crushed between the tips of the opposing teeth as the lower teeth moved upward. This wear quickly perforated the enamel. Relatively more rapidly wearing dentine was exposed (Fig. 19A), and these "windows" in the apical enamel quickly spread along the crests with continuing wear. The slightly raised edges of worn enamel enclosing the windows (Broili and Schröder, 1936: fig. 1) formed additional edges for shredding during dynamic occlusion. As the cusps were worn down, the areas for tooth-to-tooth contact increased and, consequently, occlusal pressures at the contacts decreased.

Tritylodontidae exhibit isognathly, with simultaneous occlusion on both sides, much as in certain more primitive Tritylodontoidea (Crompton, 1972: 67). Bilateral mastication is advantageous as it doubles the effective surface area for mastication and because considerable occlusal pressure can be maintained by the simultaneous action of the jaw muscles on both sides of the head (Weijs and Dantuma, 1975: 24). The unfused symphysis in tritylodontids indicates relatively little transfer of force from the working to the respective balancing side of the mandible. Mobility at the symphysis is essential for

independent and simultaneous rotation of the dentaries to align properly the opposing postcanine teeth as they sequentially come into occlusion. The quadrate was capable of the prerequisite rotation about its long axis.

The articular facet for the trochlea of the quadrate is much inclined anteromedially relative to the long axis of the articular rod. In more primitive tritylodontoids such as *Diademodon* (Grine, 1977: fig. 13), the facet has a more transverse orientation. No accessory jaw articulation is developed between the squamosal and surangular in *Kayentatherium* nor is there a contact between squamosal and dentary, *contra* Fourie (1968). These structural details are consistent with the inferred pro-palinal pattern of jaw motion. Allin (personal communication) has suggested the existence of a syndesmotomic connection between the jugal and the lateral ridge on the dentary but I find no markings on the respective bony surfaces in support of his restoration.

The principal function of the well-developed adductor jaw musculature was elevation and retraction of the mandible. By virtue of its horizontal to posteroventral fiber orientation, the posterior temporalis can be hypothesized as the principal retractor of the lower jaw. The functional importance of this muscle may account for the extension of the temporal fossa behind and below the coronoid process of the dentary. The relatively substantial increase in the height of the coronoid process, relative to the condition in *Thrinaxodon*, provided the posterior temporalis with a much increased moment arm about the jaw joint (DeMar and Barghusen, 1973). The anterior temporalis and the masseter muscles presumably acted as elevators of the mandible. The reconstructed course of the superficial masseter would indicate that a large gape could not be achieved. Protraction of the mandible during the opening phase must have been produced by the lateral pterygoids as none

of the other jaw muscles had a significant anteriorly directed vector component for this purpose.

Like that of other advanced non-mammalian synapsids, the tritylodontid masticatory apparatus features both a considerable development of the adductor jaw muscles ensheathing the coronoid process of the dentary *and* a set of greatly reduced accessory jaw bones. The joint between the articular and quadrate in tritylodontid synapsids is especially infirm and devoid of structural reinforcements against stresses produced by the jaw muscles. Crompton (1963) first emphasized this apparent enigma. He suggested the possibility of eliminating such stresses both at the jaw articulation and at the contact between the dentary and postdentary bones by a coupling of an anterodorsally aligned superficial masseter with a more or less horizontal temporalis muscle situated well above the jaw joint. These two muscles would produce a net reaction in the bite across the posterior cheek-teeth while leaving the jaw joint virtually unloaded. Tritylodontid synapsids closely approach this paradigm in the reconstructed arrangement of their adductor jaw musculature (Fig. 21). Building on recent experimental work on mammalian jaw function, Crompton and Hylander (1986) have argued that bilateral mastication was of crucial importance in minimizing the reaction forces at the jaw articulation. Hylander (1979) and Weijs (1980) have shown in a number of extant mammals that the balancing (or contralateral) jaw joint is loaded more than the working (or ipsilateral) joint during unilateral mastication. Bilateral mastication with simultaneous action of the jaw muscles on both sides, therefore, would reduce the respective loading at each jaw joint. During unilateral mastication the jaw joint on the working side would have been subjected to significant tensile forces during unilateral mastication. In terms of the bifurcal model of jaw function proposed by Bram-

ble (1978), the posterior temporalis muscle would have acted to put the jaw joint under tension. Both the masseter and anterior temporalis muscles would produce compressive loadings at the jaw articulation and, in a force coupling, would counteract the downwardly directed rotational force produced by the posterior temporalis. The incisor region was dominated by the superficial masseter, and during significant incisor loading the jaw joints would have been subjected to compression. As argued above, such large incisal bite forces were probably not required.

*Other cranial features.* It is instructive to consider briefly the distribution and degree of interdigitation of cranial sutures because they reflect both the direction and relative amount of stress affecting specific regions of the skull (Herring, 1972). The circumlacrimar region of the skull shows particularly complex sutures because it played an important role in the transmission of forces from mastication as well as from the pull of the superficial masseter. The extensively developed secondary bony palate has markedly interdigitated transverse sutures between the premaxillae and maxillae and the maxillae and palatines. The areas on either side of the mid-line sutures of the component elements are raised to form a torus. This reinforcement of the mid-palatal sutures is consistent with Tatarinov's (1963) view that the secondary palate formed a structural cross-brace within the cranial framework, in addition to separating the nasal passage from the oral cavity. Generally, the sutures that extend more or less perpendicular to the mid-line of the skull are distinctly interdigitated. The lateral walls of the braincase and the zygomatic arches must have been subjected to considerable tensile stresses produced by the contraction of the powerful jaw musculature. As noted above, the temporal fascia may have been important in aiding the zygoma in resisting tensile forces produced by the masseter muscles. The temporalis musculature,

much of which arose along the ectocranial crests, must have exerted considerable tensile forces on the wall of the braincase. This may well be reflected by the extensive ossification of this region, including the formation of considerable squamous extensions of both the prootic and epipterygoid. Various primitively extracranial vessels have been partially or completely enclosed in bone (V. capitis lateralis, vessels of the "sinus canal"), presumably to protect them from the effects of muscular contraction.

The prominent maxillary sinuses and the large spaces ventrolateral to the brain may at least in part represent "void" chambers, which could have served to lighten the massive skull.

Tritylodontid synapsids exhibit numerous cranial features that are also found in extant herbivorous mammals (DuBrul, 1977):

- shortening, deepening, and (in some cases) considerable broadening of the skull;
- deep zygomatic arch;
- jaw joint placed well above the level of the upper tooth row;
- prominent diastema between incisors and cheek-teeth;
- absence of canines;
- posterior cheek-teeth placed well back;
- origin of masseter muscles placed forward;
- dentary with tall ascending ramus.

The placement of the jaw joint well above the level of the occlusal plane, the forward shift of the masseter origin, and the posterior extension of the cheek-tooth row all serve to increase the mechanical efficiency of the jaw musculature and, therefore, the bite force across the posterior portion of the tooth row. Tritylodontids differ from mammalian herbivores in having a much expanded temporal fossa and a tall coronoid process. These differences can be related to the selective elaboration in the former of the temporalis

musculature that produced the posteriorly directed power stroke.

*Hearing.* The pronounced reduction in the size of the accessory jaw bones and the diminutive quadrate suggests that their function as elements of the jaw suspensorium was no longer their primary role. The detailed, point-by-point similarity between the postdentary bones of *Bienotherium* and the middle ear ossicles of monotremes was noted by Hopson (1966: 445). The articular with its recurved retroarticular process is directly comparable to the embryonic mammalian malleus with its recurved manubrium mallei (Fig. 23). Presley (1984: 189) expressed doubts concerning a strict homology between the retroarticular process of advanced non-mammalian synapsids and the manubrium mallei in modern mammals but his assessment was based, at least in part, on the inadequacy of preservation in previously published examples of the former feature. The similarity between the tritylodontid quadrate and the mammalian incus is not readily apparent at first glance but Hopson has argued that the peg-like posterodorsal process of the former can be compared to the crus brevis incudis. The crus longus incudis, to which the distal end of the stapes attaches, can be homologized with the posteromedially directed stapedial process of the tritylodontid quadrate. The postdentary bony rod formed an axis of rotation about which the lever arm of the retroarticular process could pivot (Hopson, 1966: fig. 8). Furthermore, the contact between the stapes and quadrate lies behind and below the axis of rotation of the quadrate, thereby creating a lever arm for that bone. This situation is directly comparable to the lever system of the mammalian auditory ossicles (Hopson, 1966: fig. 7). The quadrate pivoted about its point of attachment on the crista parotica as does the monotreme incus (Fleischer, 1973: 141).

Following Parrington (1946), Hopson (1966: fig. 6) assumed the existence of a

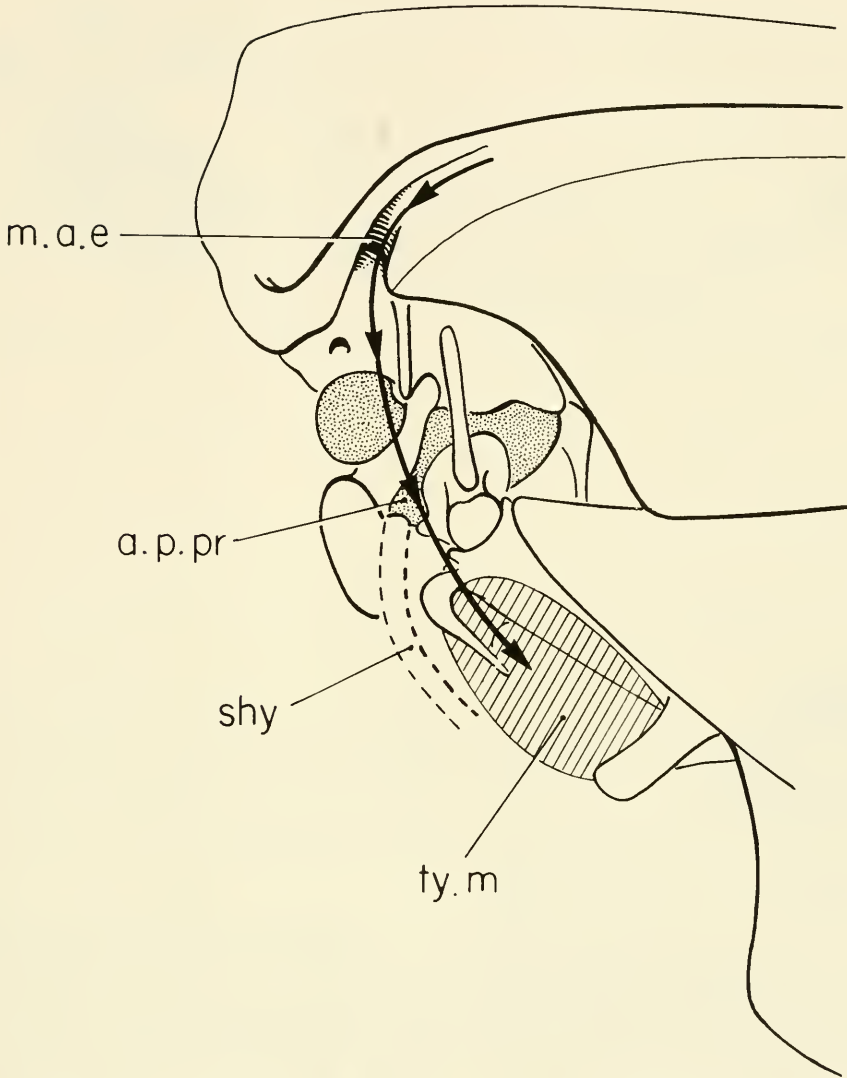


Figure 22. Diagram to illustrate the topographic relationships of the tympanic membrane (oblique hatching), external auditory meatus (arrow line), and associated bony features in *Kayenitherium wellesi*. Outline of skull based on MCZ 8812.

small post-quadratic tympanic membrane, based on the postulated course of the external auditory meatus and the alleged presence of an extrastapedial process. Allin (1975) demonstrated that there is no good evidence in support of this restoration. Indeed, as he and, more recently, Kermack *et al.* (1981: 112) have argued,

such a tympanum would be extremely inefficient in receiving air-borne sound because its area would have been tiny relative to that of the fenestra ovalis. Allin instead postulated the existence of a tympanic membrane attached to the reflected lamina of the angular and to the retroarticular process. He hypothesized a con-

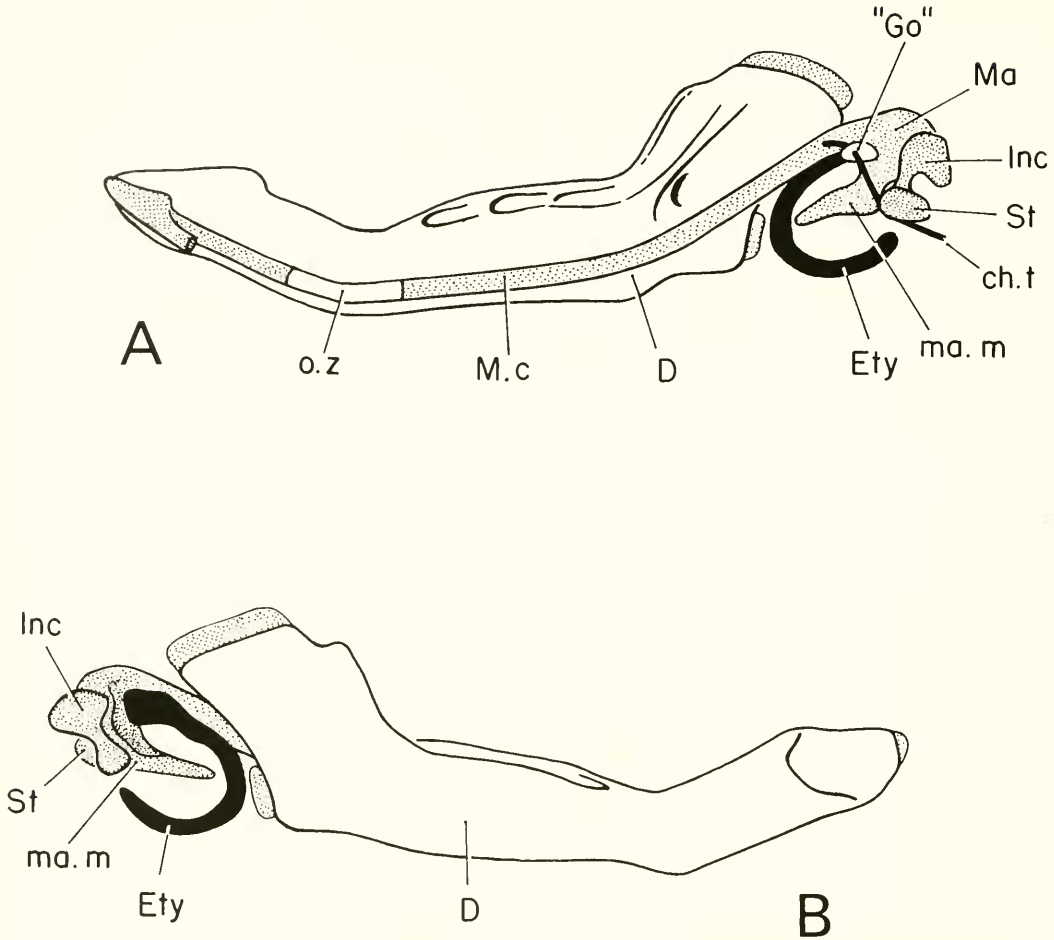


Figure 23. Outline drawings of the lower jaw, Meckel's cartilage, and associated structures in a rabbit embryo (greatest length: 45 mm), based on a model prepared by E. Gaupp. A) medial view. B) lateral view.

*Abbreviations:* ch.t, chorda tympani (VII); D, dentary; Ety, ectotympanic; "Go," "gonial" ossification; Inc, incus; Ma, malleus; ma.m, manubrium mallei; M.c, Meckel's cartilage; o.z, ossified zone; St, stapes. Compare with Figure 22.

ducting chain consisting of angular, articular, quadrate and stapes. Tympanic vibrations would produce a force acting on the distal extremity of the retroarticular process, initiating small rotational movements about its long axis that were transmitted to the quadrate. The quadrate would rotate slightly about its long axis and thereby activate the stapes. Angular and articular complex presumably vibrated as a unit, much as in monotremes (Aitkin and Johnstone, 1972: 247). Because of its stiffness and mass this system of

auditory ossicles would still be rather inefficient and probably worked effectively only at frequencies below one kilohertz. Indirect sound conduction from the substrate via the snout and hyoid apparatus may have been significant in addition, particularly if the hyoid arch supported the tympanic membrane posteriorly (Presley, 1984: fig. 1). The external auditory meatus, lodged in the squamosal sulcus, presumably carried on forward and below from the ventral termination of the bony sulcus (Presley, 1977; Fig. 22).



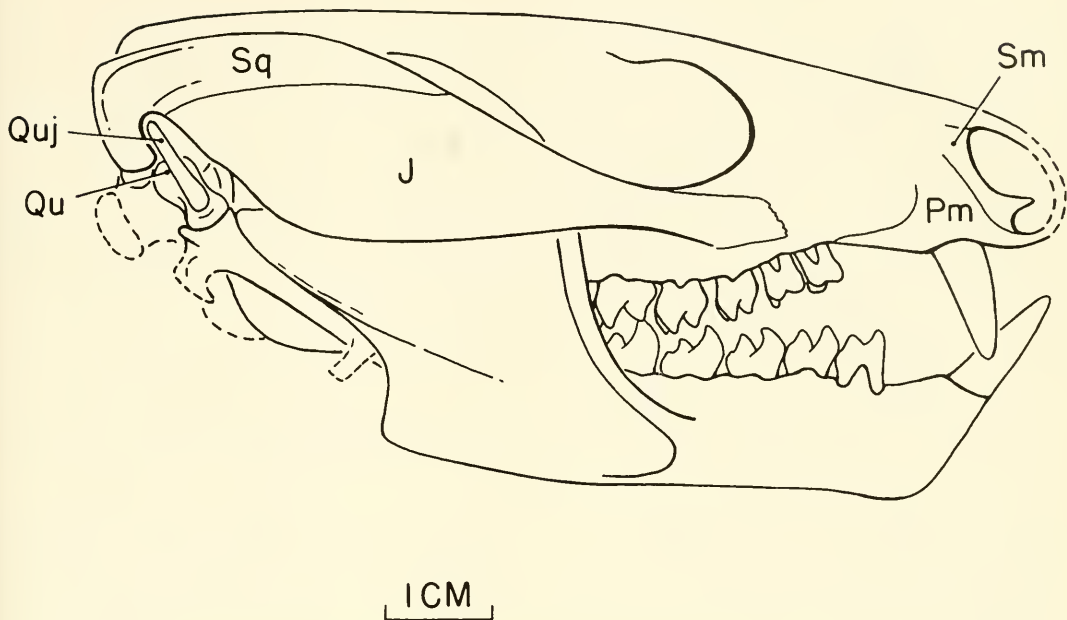


Figure 24. Skull of *Kayentatherium wellsi*, USNM 317203, reconstructed in right lateral view.

If the above restoration of the auditory complex is accurate, the tritylodontid system of sound transmission had developed a level of organization directly comparable to that of the most primitive known mammals, as inferred by Kermack *et al.* (1981).

#### POSSIBLE JUVENILE SPECIMENS AND RANGE IN SIZE

Among the numerous remains of small specimens of Tritylodontidae from the Kayenta Formation, a few appear to represent juvenile specimens of *Dinnebitodon* and *Kayentatherium*. Most of the other small tritylodontid remains are referable to *Oligokyphus* on the basis of dental characters (Sues, 1985b).

MCZ 8847, a right jugal and attached fragmentary maxilla with three postcanine teeth, may represent an early ontogenetic stage of *Dinnebitodon*. Its maximum length along the outer margin is 15 mm. The postcanine teeth have two buccal, three median, and two lingual cusps (Sues, 1985b: fig. 5C). The anterolingual

cusps is much smaller than its successor. The completely preserved jugal closely resembles that of *Kayentatherium* (MCZ 8812, Fig. 1) in shape. The arrangement of cusps supports reference to *Dinnebitodon* rather than to *Oligokyphus* (Sues, 1985b). If correctly identified, MCZ 8847 would represent the smallest known individual of that taxon.

The upper postcanine tooth MCZ 8847 and two still uncatalogued teeth (field-numbers AR81/152 and AR81/209) have two buccal, three median, and three lingual cusps and may be referable to *Kayentatherium*.

The small dentaries MCZ 8845 and MCZ 8848 (Fig. 26A) have distinctly pointed angular processes and postcanine teeth with two principal cusps in each row. They are clearly different from the dentaries referred to *Oligokyphus* in these features (Sues, 1985b). MCZ 8848, a left dentary, is beautifully preserved. It holds two incisors, the anterior one of which is large and procumbent whereas the posterior one is smaller and less procumbent

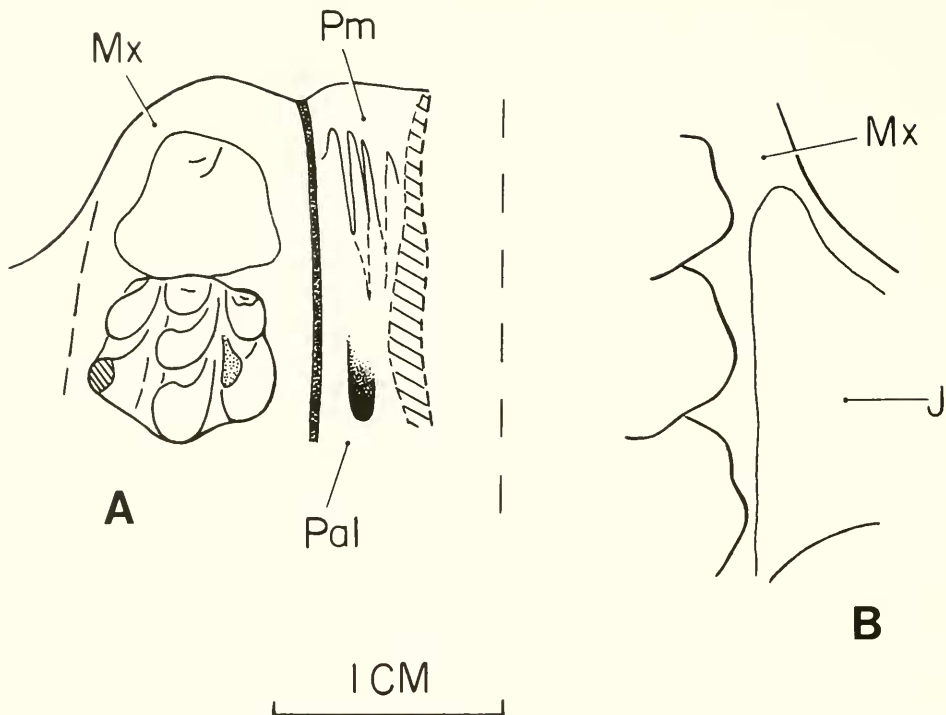


Figure 25. *Dinnebitodon amarali*, MCZ 8830. A) contact between right maxilla, palatine, and premaxilla on the palate as preserved. B) sutural contact between left jugal and maxilla in ventral view.

than its predecessor. The coronoid process slopes backward and its height equals the distance from the ventral projection of the symphysis to the angular process. The articular process is proportionately large. MCZ 8845 and MCZ 8848 possibly represent very young specimens of either *Dinnebitodon* or *Kayentatherium*.

Two tiny dentaries, MCZ 8849 (length from symphysis to angle about 6 mm) and MNA V3241 (Fig. 26B) are probably the smallest known non-mammalian synapsid jaws. They already show all the structural features characteristic of tritylodontid jaws. MCZ 8849 holds a large procumbent incisor and two postcanine teeth. The anterior cheek-tooth is raised well above the more posterior one and its anterolingual cusp is displaced forward relative to the anterobuccal cusp as on some teeth of *Oligokyphus* (Kühne, 1956: 80). MCZ 8849 and MNA V3241 represent extremely im-

mature individuals, perhaps hatchlings. Their taxonomic affinities cannot be determined at present owing to the absence of clearly diagnostic features.

One of the specimens described by D. M. Kermack (1982: 7) but not included in her hypodigm for *Kayentatherium wellesi* was a fragment of a very large dentary. Kermack left its taxonomic status uncertain because of the considerable size difference to the holotype of *K. wellesi* (UCMP 83671). As Kermack herself noted, comparable size differences are found among modern crocodiles. The larger sample for *Kayentatherium* used in this study clearly demonstrates a range in skull length from about 80 mm (USNM 317203; Fig. 24) to about 260 mm (MCZ 8812; Fig. 1) without any structural differences of diagnostic significance. Dodson (1975: 317) observed a range in skull length in a sample of 52 skulls of *Alligator mississippi-*

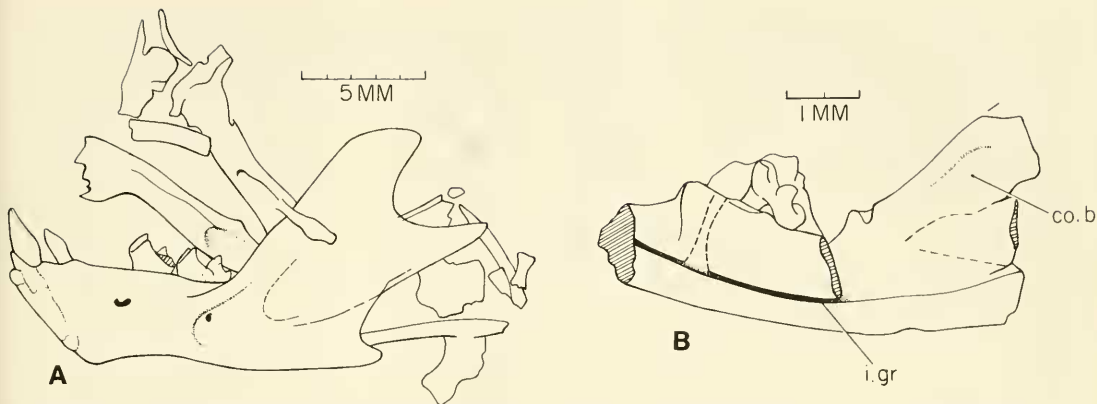


Figure 26. Juvenile specimens of indeterminate Tritylodontidae from the Kayenta Formation. A) MCZ 8848, left dentary in lateral view, with associated (?) postdentary elements. B) MNA V3241, right dentary in medial view.

*piensis* from 35.3 mm to 632 mm. *Bienotherium* shows size differences comparable to *Kayentatherium*. Chow (1962) described two fragmentary maxillae of *Bienotherium* and (admittedly tentatively) referred them to a new species, *B. magnum*. He notes that the length of the upper tooth row (c. 76 mm) is "almost twice that in *Bienotherium yunnanense*." This difference in size is almost identical to that between specimens MCZ 8811 and MCZ 8812 of *Kayentatherium*. *Bienotherium magnum* can, therefore, be synonymized with *B. yunnanense*. Hopson and Kitching (1972) have reached similar conclusions concerning the synonymy of *Likhoelia* Ginsburg, 1961 and *Tritylodontoideus* Fourie, 1962 with *Tritylodon* Owen, 1884 from the Stormberg Group of southern Africa. Tritylodontid synapsids apparently had a typically "reptilian" pattern of more or less continuous growth throughout life.

#### RELATIONSHIPS OF KAYENTATHERIUM AND DINNEBITODON

The Tritylodontoidea *sensu* Hopson and Kitching (1972) are characterized by the possession of postcanine teeth with buccolingually expanded crowns, which meet in complex occlusion, and by the deep

dorsal emargination of the occipital portion of the squamosal (convergent with Chiniquodontidae). This represents a minimal definition of the group, which reflects the paucity of comprehensive anatomical information concerning the majority of advanced non-mammalian synapsids. Certain other diagnostic features listed by Hopson and Kitching (1972) are also found in *Cynognathus*, which Kemp (1979) placed as the sister-taxon of *Diademodon*. The Tritylodontidae Cope, 1884 (including Bienotheriidae Young, 1940) form a strictly monophyletic taxon, which can be defined by a set of derived craniodental features (Hopson and Kitching, 1972; Sues, 1986b):

- second upper and first lower incisors greatly enlarged;
- first lower incisor procumbent;
- canines absent;
- postcanine teeth with multiple roots;
- upper postcanine teeth with three and lower postcanine teeth with two antero-posterior rows of crescent-shaped cusps;
- prefrontal and postorbital (and postorbital bar) absent;
- articulation between quadrate and anterior paroccipital process (crista parotica) *without* contact between quadrate and squamosal (with the possible exception of *Oligokyphus*).

Clark and Hopson (1985) and Sues (1986b) have reviewed the interrelationships of tritylodontid genera. *Kayentatherium* most closely resembles *Bienotherium* Young, 1940 from the Lower Lufeng Series of Yunnan, China. It is distinguished from the latter genus as well as from all other known Tritylodontidae by the presence of a single upper incisor, rather than two or three, in each premaxilla. *Nearctylodon broomi* Lewis, 1986 is clearly a junior synonym of *Kayentatherium wellsi* D. M. Kermack, 1982, based on the presence of a single incisor in each premaxilla and the structure of the upper postcanine teeth (personal observation). Further craniological comparisons between *Kayentatherium* and *Bienotherium* must await publication of Hopson's monographic revision of the latter genus. Certain differences in the upper postcanine teeth enumerated by D. M. Kermack (1982) are not valid (Sues, 1986b). *Dinnebitodon* apparently belongs to a more advanced clade including *Bienotheroides* Young, 1982 (upper Sha-Xi-Miao Formation, Sichuan, China) and *Bocatherium* Clark and Hopson, 1985 (La Boca Formation, Mexico). *Bienotheroides* is either late Mid-Jurassic or early Late Jurassic in age but no reliable age estimate can as yet be offered for *Bocatherium*. Derived features shared by members of this clade, which probably also includes the poorly known *Stereognathus* Charlesworth, 1855 from the Middle Jurassic (Bathonian) of the British Isles (Hopson, personal communication), are (1) exclusion of the maxilla from the side of the face by the enlarged premaxilla and lacrimal, (2) complete lateral overlap of the maxilla by the jugal (which extends down to the level of the upper tooth row), and (3) contact of the palatine and premaxilla on the palate, excluding the maxilla from participation in the formation of the secondary bony palate (Sun, 1984; Clark and Hopson, 1985; Sues, 1986a,b). Character (3) is foreshadowed to some extent in juvenile specimens of *Kayentatherium* (MCZ 8811, Fig. 6) where the premaxilla

extends back on the palate between the first upper postcanine teeth. Adult specimens (MCZ 8812, MNA V3141), however, are closely similar to *Bienotherium* in that the palatal suture between the premaxilla and maxilla is placed well anterior to the upper cheek-teeth. The genera of the *Bienotheroides* clade variously show reduction in the number of cusps on the upper postcanine teeth. The upper postcanine teeth of *Dinnebitodon* can be distinguished from those of *Bienotheroides* and *Bocatherium* by the presence of but two lingual cusps and from those of *Stereognathus* by the retention of three median cusps.

## APPENDIX

### Abbreviations Used in Figures

An	angular
ANT	anterior
Art	articular
AT	M. temporalis, pars anterior
a.l.pro	anterior lamina of prootic
a.q.f.	anterior facet on quadrate
a.p.pr	anterior paroccipital process (crista parotica)
al.ps	parasphenoid wing
an.p	angular process of dentary
ar.c	articular complex
art.eo	articular facet for exoccipital
art.f	articular facet for quadrate trochlea
art.p	articular process of dentary
art.pro	articular facet for prootic
Bo	basioccipital
Bs	basisphenoid
BUC	buccal
Co	coronoid
Co.o	occipital condyle
c.i.o	infraorbital canal
c.i.o.l	"lacrimal branch" of infraorbital canal
c.r.t	crypt for replacement teeth
c.sm	canal in septomaxilla
co.b	boss for coronoid
co.p	coronoid process of dentary
cr.sa	sagittal crest
D	dentary